Reproductive costs

and their expression in the common guillemot

Uria aalge

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CANDIDATE'S DECLARATION

I declare that the work recorded in this thesis is entirely my own, unless otherwise stated, and that it is of my own composition. No part of this work has been submitted for any other degree.

T.I. Van Pelt

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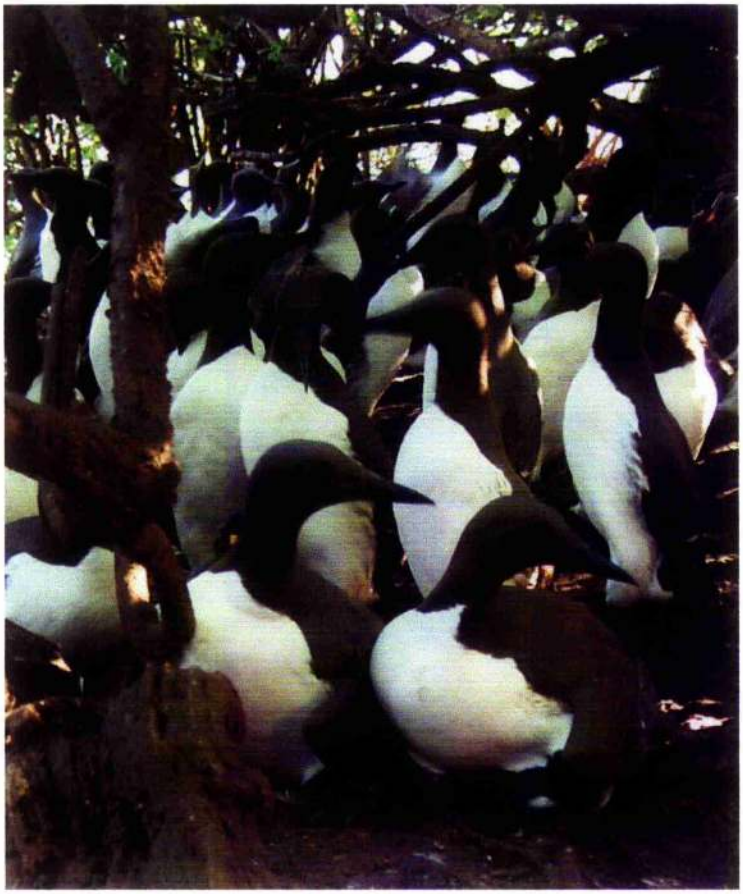

Frontispiece: Common guillemots *Uria aalge*, nesting amongst 'inland' habitat (see Methods, Chapter Five) on Duck Island, Alaska, in 1999.

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SUMMARY

I present studies on reproductive costs in common guillemots *Uria aalge*, framed against a background of data from a larger study that provides context for feeding and breeding conditions dominating the study colonies. The components of seasonal declines in reproductive performance were examined at a colony breeding under consistently demanding conditions, in an effort to assess whether previously documented costs of breeding late in the season are expressed relatively strongly under poor conditions. I found the expected seasonal declines in egg quality and overall reproductive success. However, hatching success and offspring quality appeared to remain equal across the season. I discuss the interpretations of my correlative results.

The relationship between reproductive performance and parental and offspring body condition is examined, using data from two years with contrasting productivity at a single colony, and data from two colonies with contrasting productivity in a single year. Adult and offspring condition was decoupled from inter-year productivity at one colony, and inversely related to productivity when compared between colonies. I tentatively conclude that a combination of colony-specific factors and the long-term integration of patterns of resource allocation in this long-lived seabird prohibit the simplistic use of body condition as an indicator of reproductive effort or investment.

I present results of a manipulative experimental increase in egg production costs, carried out at a colony breeding under poor conditions. Compared to birds laying first eggs at the same time, reproductive success was sharply reduced in parents induced to lay replacement eggs, especially in naturally late-laying birds. Replacement eggs were smaller, but proximate composition did not differ, and chicks from replacement eggs grew as well as those from first eggs. My results demonstrate a strong state-dependence in replacement laying success.

CHAPTER ONE

GENERAL INTRODUCTION

General Introduction

This thesis comprises investigations into the costs of reproduction. Ever since Darwin (1859) introduced the concept of variation in reproductive success as the mechanism of evolution, there has been considerable interest in the factors that underpin variation in breeding performance. The fact that organisms do not constantly reproduce implies that reproduction is costly. However, formal evaluation of reproductive costs in the late 19th and early 20th centuries consisted for the most part of studying the proximate factors that restrict annual reproduction, and classifying the vast array of reproductive strategies employed by animals, with little in the way of a theoretical framework being developed.

Change came in the mid-20th century, with a substantial expansion in investigations of the way major events are distributed over the lifetimes of individuals, formalised as the study of life histories (reviewed in Ricklefs 2000). That some of the effort allocated by parents to the production and growth of their offspring comes with a penalty paid by a reduction in future productivity – manifestation of the 'cost of reproduction'- is an idea first elucidated in a life-history context by Williams (1966). It was later expanded by Trivers (1972), who coined the term 'parental investment'. Differential parental investment controls the relative levels of current versus future reproduction. This can be viewed as a constrained evolutionary response when integrated with the concept introduced by Cody (1966) of the allocation of limited resources, whereby the response (allocation between current and future reproduction) is driven by constraints (limited resources) towards evolutionary optimisation of lifetime reproductive success.

Reproductive costs therefore represent a fundamental type of 'trade-off'- the negative relationships between allocation patterns that shape the simultaneous evolution of two traits (Stearns 1992). Given limited resources, energy expended on current reproduction may be traded off against investment in somatic growth or other self-maintenance, forming a link to a potential reduction in future reproduction. The balance of this trade-off is dependent in part on lineage-specific factors (Drent & Daan 1980), with variation in physiological ecology (e.g. growth rates as a function of body size; energy required per gram of offspring, etc.) defining optimal reproductive investment. In heterogeneous environments, variation in an individual organism's physiological and environmental conditions is an additional factor that drives the strategic decisions made over an animal's lifetime. Such variation is referred to as the 'state' of an organism, and forms the basis for the concept of an individual's state-dependent optimisation of life-history decisions (such as level of parental investment; McNamara and Houston 1996).

Some of the fundamental evidence for the trade-off between current and future reproduction has come from laboratory studies of easily manipulated organisms- Partridge and Farquhar (1981), studying fruit flies *Drosophila* sp., and Snell and King (1977), studying rotifers *Asplanchna* sp., supplied evidence that reproduction can reduce future survival (and thus reproduction). Beyond the laboratory, in studies of natural variation in annual meadow grasses Law *et al.* (1979) found a strong negative correlation between the number of inflorescences produced in the first and second reproductive season. Using field manipulations of predation levels on guppy *Poecilia reticulata* populations, Reznick and colleagues (1990) observed significant evolutionary responses such as changes in male age and size at maturity and offspring mass; these changes were in the direction predicted to optimise lifetime

reproduction, providing a case study for further understanding of the trade-off between current and future reproduction.

In part due to their visibility and accessibility, and also to the long tradition of previous work in avian breeding systems (Lack 1968), the study of birds has proven particularly fruitful for understanding reproductive trade-offs. Avian species are characterised by a wide range of life-history strategies, increasing the power of interpreting correlative evidence. Birds also generally reproduce more than once, and in discrete phases, facilitating study of within- and between-season variation in reproductive allocation (Monaghan & Nager 1997). However, in long-lived species such as birds, the nature of reproductive trade-offs can also be relatively difficult to uncover, since they represent patterns of resource allocation that are integrated across lifetimes (Cooch & Ricklefs 1994). Trade-offs have been measured as correlations in the field, phenotypic correlations in the laboratory, genetic correlations, and as phenotypic manipulations (i.e. experiments) in the field (Stearns 1992). In birds and other organisms, experiments have proven crucial to conclusively understanding trade-offs (Lessels 1991; Daan & Tinbergen 1997). Correlative data cannot be used to prove causation, and phenotypic correlations between and within species could mask or artificially amplify underlying trade-offs (Svensson & Nilsson 1995). Quality effects could covary with other traits being measured, forcing positive rather than negative relationships. Examples of successful phenotypic manipulations include work by Brinkhof *et al.* (1997), showing how optimal seasonal timing of reproduction is based on the trade-off between current and future reproduction, with reproductive timing balancing parental effort (and thus future survival) with optimised offspring fitness. Sinervo *et al.* (1992) used experimental manipulations of yolk mass in lizard eggs to demonstrate a positive correlation between relative yolk mass and survival among broods.

An important consideration in interpreting phenotypic expressions of reproductive trade-offs is that they often appear only under food stress (Stearns 1992). Trade-offs assume limiting resources, but may be difficult to demonstrate in favourable environmental conditions or in high quality individuals. Some reproductive costs or benefits may be experimentally altered without a corresponding trade-off, due to some behavioural buffering (Burger & Piatt 1990). Conversely, in a resource-poor state, trade-offs are more likely to be exposed (Stearns 1992).

The work presented in this thesis uses both correlative and experimental approaches to investigating aspects of reproductive costs. I worked at both a relatively food-poor colony and a relatively food-rich colony (see General Methods) of common guillemots *Uria aalge*, long-lived (up to 25 years) seabirds whose clutch size of one simplifies evaluation of parental investment. Chapter Three examines the seasonal variation in breeding performance at these colonies. By quantifying the seasonal trends in i) reproductive output, and ii) offspring condition, answers to two questions were sought: 1) do birds breeding in a relatively resource-poor state exhibit relatively strong seasonal declines in reproductive output? and 2) what is the link between seasonal declines in simple output and the variation in offspring quality? Although this correlative work has limited implications, it provides some context for understanding reproductive strategies in this study system.

Chapter Four examines the relationship between productivity and both parental and offspring body condition. Mean levels of reproductive output over the three phases of breeding at the two different guillemot colonies were measured, in two different years. Productivity was used as an index of mean population reproductive effort, and then compared effort with data on adult and fledgling body condition. The condition of individuals is often used as an index of costs and assumes

that changes in reproductive effort will be reflected in a condition change. In this context, three questions were asked: 1) how is productivity related to adult body condition, and, given some relationship, is it consistent within and between colonies?, 2) is there a sex difference in the expression of links between productivity and adult body condition?, and 3) how is productivity related to offspring body condition? The results illustrate the complexities in understanding linkages in unmanipulated natural systems.

In Chapter Five, the results of phenotypic manipulations of costs are presented, in the form of an experimental increase in egg laying investment. Egg loss is a persistent feature of many reproductive environments, and the decision whether or not to replace the lost egg, and how much of a parent's limited resources to invest in that egg, can be an important component in determining an individual's lifetime reproductive success. Recent studies have shown that i) egg production and incubation can impose fitness costs on both parents and offspring (Monaghan & Nager 1997); and ii) the probability and success of replacement laying is determined more strongly by individual quality than by environmental deterioration (Hipfner 1997; Hipfner *et al.* 1999). It was hypothesised that the extent to which even relatively high-quality individuals can compensate for the added costs of replacement laying varies with environmental conditions, leading to the prediction that increased investment at the egg stage would carry a relatively high fitness cost among individuals breeding in a poor state at this colony.

In Chapter Six, a general discussion of my results is presented. The findings are interpreted in the context of reproductive costs and trade-offs, the limitations of the interpretations are addressed, and some conservation applications of this work are proposed.

CHAPTER TWO

GENERAL METHODS

General Methods

Study location and background

This work was conducted at two common guillemot *Uria aalge* colonies in Cook Inlet, Alaska, between June-September in 1998-1999. The common guillemot is a highly colonial seabird with a circumpolar boreal and low-Arctic distribution. Only one egg is laid (although lost eggs may be replaced; Chapter Five) and both sexes share incubation and chick provisioning. The chick is fed at the nest for 15-30 days, leaves the colony at < 30% of adult mass, and is subsequently cared for by its male parent for up to six weeks (Gaston & Jones 1998).

The colony at Duck Island (west side of Cook Inlet; 60° 09′ N, 152° 34′ W) currently supports ca. 2500 guillemots, representing a steady decline to ca. 10-20% of maximum counts made in the early 1970s, while the Gull Island colony (east side of Cook Inlet; 59° 35′ N, 151° 19′ W) has expanded over the same time period, and currently supports ca. 8000 guillemots. The two colonies are separated by 100 km and are in oceanographically distinct habitats (Robards *et al.* 1999). A number of independent measures made concurrently with this study (nearshore forage fish abundance; offshore midwater fish availability; adult foraging trip duration and 'loafing' time at the nest; stress hormone levels) provide strong evidence that guillemots breeding at Duck Island experienced food shortages during the 1995-1999 breeding seasons and are relatively highly stressed, while guillemots breeding at Gull Island experienced relatively greater prey availability and lower stress (Kitaysky *et al.* 1999; Robards *et al.* 1999; Zador & Piatt 1999; J.F. Piatt *et al.*, unpublished data).

Furthermore, at-sea surveys show that birds breeding at Duck Island must travel further to access prey (Piatt *et al.* unpubl. data). However, over five years of study (1995-1999), the reproductive success of guillemots at Gull Island has been lower, on average, than that of guillemots at Duck Island (Piatt *et al.* unpubl. data).

Egg loss through predation is not uncommon at these colonies. Each supports a colony of ca. 500 glaucous-winged gulls (*Larus glaucescens*) and is regularly visited to varying degrees by ravens (*Corvus corax*), bald eagles (*Haeliatus leucocephalus*), and peregrine falcons (*Falco peregrinus*). Gulls and ravens in particular were regularly observed predating guillemot eggs; eagles and falcons took eggs directly to a lesser extent, but also facilitated gull and raven egg predation by flushing adults off their nesting areas.

Timing and productivity

Breeding chronology and breeding success of common guillemots were monitored following a modified version of the Type I protocols detailed by Birkhead and Nettleship (1980). Using digital colour photographs or hand-drawn sketches, each site where a guillemot was present in the pre-laying period was mapped. Plots were visited every fourth day, and the presence and posture (e.g. standing, incubating, brooding) of the nesting adults was recorded. The 3 d intervals between visits means that all dates presented in this paper are accurate to within at least 3 d and have error of +/- 2 days; however, the error was assumed to be normally distributed and thus not to affect the analyses presented here. Laying date was defined as the first day we either recorded an adult in an incubating posture or saw an egg at a site where there

had not been one on the previous visit. Because guillemots incubate their eggs very tightly, only rarely revealing the egg to observers, it was necessary to infer some egg-laying dates based on first recording of incubating posture at sites where an adult was observed in an incubating posture on at least three consecutive visits (Murphy & Schauer 1996). For those sites that already had an adult in incubating posture or an egg present when first visited or mapped, laying date was back-calculated from hatch date, using the normal incubation period of 33 d (Birkhead & Nettleship 1987; Gaston & Jones 1998). This method appeared to be reliable, as it correctly forward-predicted hatching date (+/- 2 d) at most sites where laying date was known.

The presence of just-hatched chicks can also be difficult to determine directly. Hatching date was therefore similarly defined as the first day we either recorded an adult in brooding posture or saw a chick at a site where there had not been one on the previous visit. Fledging age is defined as the inclusive number of days from the hatching date to the day prior to the date when the chick was first recorded as not present. After colony departure, chicks continue to be cared for by the male parent for up to two months (Varoujean *et al.* 1979), but for convenience here, and following other studies of this species, chick departure from the nest site is taken as 'fledging', and chicks that have departed the nest site as 'fledglings'. Since 15 days is the minimum nest departure age in common guillemots (Gaston & Jones 1998), chicks were considered to have 'fledged' successfully if they disappeared from the nest site >= 15 d after hatching; any chicks that disappeared prior to this were assumed to have died.

Hatching success is taken as the proportion of active nest sites (sites where the presence of an egg was either inferred or directly observed) that produced a chick, and reproductive success the proportion of active nest sites that fledged a chick (Birkhead & Nettleship 1980). As documented in other studies of guillemot productivity, we witnessed one female guillemot losing her egg immediately after laying, and noted evidence of egg predation from unknown nests on many other occasions. Thus it can be assumed that some guillemot pairs laid and lost their egg in the 3 d interval between any two successive observation days, implying that the measurements of both hatching and breeding success represent overestimates (Boekelheide *et al.* 1990); however, because our observation effort was constant during the season, any overestimates should also be constant and should not affect the trends documented here. For those nest sites where the first egg was lost and a second egg was laid, the laying date of the first egg was used in relation to the success of the second egg (but see Chapter Five for methods of a more detailed study on replacement laying). Fledging success is defined as the proportion of hatched chicks that fledged successfully. Reproductive success is taken as the proportion of nest sites where an egg was laid from which a chick fledged.

Egg size and quality

To obtain data on egg size in relation to laying date, daily checks of a separate group of nest sites at Duck Island were carried out using similar protocols to those already described. These nest sites were observed from a hide located 1-10 m from ca. 150 inland nest sites. After incubation was confirmed, an egg-grabbing tool was used to

remove eggs with known laying dates. The tool was a 'Helping Hand' (designed as a grasping extension for people with limited mobility), modified with padded jaws and attached to a telescoping 8 m fibreglass pole. The claw's trigger was fitted with a trailing line, allowed us to remain concealed while seizing eggs up to 7 m from the hide, minimising colony disturbance. Parental reaction to egg removals varied widely, but the majority of attending parents remained in contact with their nest site during egg-removal bouts, and parental behaviour in the targeted sub-colony normalised after ca. 1 hour. Egg-predating glaucous-winged gulls were kept away from eggs left unprotected during removal activities by judicious use of thrown pebbles or sticks. The length and maximum breadth of each removed egg (+/- 0.1 mm) was measured using callipers. Egg volume indices were calculated using the formula (length*breadth^2; Birkhead & Nettleship 1984).

Fresh eggs were boiled for ca. 12 min within 48 h of collection, placed inside a plastic bag, and stored in a freezer until later analysis of composition. In the laboratory, each egg was weighed, then thawed and separated into shell, yolk, and albumen. Each component was dried separately at 60°C to constant mass. Components were reweighed to determine dry mass and percent water content. Since nearly all egg lipid is contained in the yolk (Carey 1996), the lipid content of the yolk only was measured. Lipid was extracted from the yolk using Soxhlet extraction with petroleum ether as a solvent (Dobush *et al.* 1985). Samples were then dried again and reweighed, and lipid content determined by subtraction. The boiling and freezing processes altered egg water content, and therefore comparisons are presented in dry mass terms only.

Chick growth

Due to the excessive colony disturbance involved in chick captures, it was not possible to repeatedly capture individual chicks. Two alternative approaches to compare chick growth were therefore used; structural size in relation to age, and mean body condition.

Chicks were captured using a fibreglass pole and wire hook once during the linear growth phase (4-14 days). Chick capturing bouts were timed to minimise disturbance whilst ensuring the necessary variation in growth stage for calculation of growth rates; weight (g), head-plus-bill, tarsus, and wing lengths (to longest primary covert) were measured in millimetres. After processing, chicks were returned to the vicinity of their nest site using the same tool. Most chicks were reunited with their parent after <10 min.

To obtain an index of body size for chicks, a principal components analysis (PCA) was performed on the linear measurements (Freeman & Jackson 1990). Measurement data were multiplied by the coefficients, and added together to produce a PCA factor score for each chick, hereafter called the 'body size index'. Body size indices were regressed on the age (days) of known-age chicks to measure structural growth rate within and between groups. Regression slopes (representing growth rate) and elevations were compared using ANCOVA. Body mass (grams) of chicks was then regressed on the body size index to generate an equation predicting the mass of a chick, given a known size. Residuals expressed as a percentage of the

predicted mass were then used to calculate a condition index (Golet & Irons 1999; Jakob *et al.* 1996).

Adult condition

Breeding adults were captured using a telescoping fibreglass pole fitted with a noose. All birds captured were actively attending a nest site, egg, or chick. Captured birds were ringed with a unique combination of colour rings and a metal USFWS ring, and a small blood sample for sex determination was taken from the wing. Blood was collected and stored in a 1.8 ml vial that had been pre-filled with a buffering solution. The sex of the bird was later identified from red blood cell DNA, using two *CHD* genes (Griffiths *et al.* 1996). Body mass (± 5 g) was measured using spring scales; head-plus-bill and tarsus length ± 1 mm using vernier callipers; and flattened standard wing length ± 1 mm (carpus to distal end of longest primary feather) using a stopped ruler.

To obtain an index of body size for adults, a principal components analysis (PCA) was carried out on the linear measurements of all captured adults (Freeman & Jackson 1990). As with chicks, measurement data were multiplied by the coefficients, and added together to produce a PCA factor score for each adult, hereafter called the 'body size index'. Mass was then plotted against the body size index; the resulting least-squares regression equation predicts mass for an adult of a given size. Residuals from this regression were used (expressed as a percentage by which a bird's actual mass differs from predicted mass) as an index of individual adult condition (hereafter called 'body condition'; Golet & Irons 1999; Jakob *et al.* 1996).

For some analyses, capture dates were standardised relative to the median chick hatching date (MCHD) of each colony-year, and grouped into three phases of breeding: Prelaying (>32 d prior to MCHD); Incubation (between -32 d and MCHD); and Chick rearing (dates greater than MCHD).

Fledgling condition

Fledging chicks were captured as they made their way across cliff-base rocks toward the ocean. Captures were timed to overlap with the peak in numbers of fledglings. Mass (± 1 g) was measured using a spring scale, and flattened standard wing length ± 1 mm (from the carpus to tip of the longest feather). Processing each fledgling generally took no longer than 1 minute, and fledgling behaviour post-handling appeared to be no different from fledglings that were not captured.

Age of fledglings was estimated using a wing length-age regression determined from known-age chicks (see Chapter Five). Using body size to estimate offspring age can be imprecise (Cooch *et al.* 1999); therefore estimated ages were compared with ages determined by chick departure from nest-sites in observed plots. Fledgling body condition was expressed as a size-corrected index by dividing mass by wing length, hereafter called 'body condition'.

Ethical note

All captures were carried out under the authority of permits issued by the US Fish and Wildlife Service and the Alaska Department of Fish and Game. Handling times were minimised wherever possible to reduce the stress of capture.

Statistical analyses

Statistical analyses were carried out using SPSS (version 7) software. Seasonal trends in hatching success, fledging success, and breeding success were analysed using logistic regression and log-likelihood ratio tests. Linear regression was used to analyse seasonal variation in egg volume, mass, and fledging age and condition.

We compared adult condition in relation to sex, colony, and year using two- and three-way ANOVAs; where significant effects were found, we used Sheffé's multiple comparison tests. The relationships between fledgling wing length and mass were compared between colonies and years with ANCOVA. Student's *t*-tests were used to compare fledgling means between colonies and years, after ensuring that the assumptions of approximate normality were met and assuming equal or unequal variances as appropriate. Analyses were carried out using SPSS; all tests are two-tailed and considered significant at probability levels less than $\alpha = 0.05$. Means are given $\pm$ 1 SE.

Chapter Three

Seasonal trends in the reproductive performance of common guillemots *Uria aalge*

Introduction

For animal species with distinct breeding seasons, variation in breeding success in relation to the timing of breeding within a season is common. Avian reproductive success is particularly variable and visible, and has consequently attracted a great deal of interest among ecologists. Following study in a range of avian families, it is now generally recognised that reproductive success in birds tends to decline as the breeding season progresses, with early-laying pairs often producing larger clutches, raising a greater number of fledglings, and eventually recruiting more of their fledglings into the breeding population (e.g. Hedgren & Linnman 1979; Drent & Daan 1980; Hannon *et al.* 1988; Hochachka 1990; Brouwer *et al.* 1995). However, breeding too early in the season can carry a cost, shown for example in terms of reduced fledging success and female overwinter survival (Nilsson 1994), suggesting some optimal time of breeding contingent on interactions between the quality of the parents (Aparicio 1998), food availability (Daan *et al.* 1988), and potential number of broods raised per season (Svensson 1995).

Colonial birds face an additional seasonal constraint imposed by the importance of synchronous reproduction. The majority of seabird species are colonial breeders; this can be partly explained as an adaptation for maximising fitness by a combination of more efficient foraging and 'predator swamping', such that the per individual productivity is increased and risk of predation is reduced (Birkhead 1985). However, the predation-related benefits of coloniality are strongly affected by the degree of synchrony in reproduction (Birkhead 1977), since the benefits of predator swamping for an individual breeding either earlier or later than its neighbours are reduced, while the costs of predator attraction remain unchanged. Egg laying in colonial seabirds thus tends to be closely synchronised (Lack 1968), and flexible fledging ages

in some seabirds may be at least partially adapted to increase synchrony in fledging despite variation in laying date or delayed laying due to replacement of a lost egg (Gaston & Nettleship 1981; Hipfner & Gaston 1999a).

Most seabird species have a clutch size of one; this is thought to reflect the difficulty of provisioning their young in marine habitats characterised by patchy, distant prey. Parental adjustment of annual reproductive investment is thus initially limited to egg size and quality. A seasonal decline in egg size has been documented in many seabird species (reviewed in Moreno 1998). Egg size has been shown to affect both parental and offspring fitness in various taxa, but in birds the relationship between egg size and offspring quality remains equivocal (Williams 1994; Bernardo 1996; Hipfner 2000); other aspects of the egg, such as nutrient content, may be important (Nager *et al.* 2000).

Colonial common guillemots *Uria aalge* and the closely related Brünnich's guillemots *Uria lomvia* have been the subject of numerous studies examining seasonal changes in reproductive output (e.g. Birkhead 1977; Gaston & Nettleship 1981; Wanless & Harris 1988; Boekelheide *et al.* 1990; Hatchwell 1991; Murphy & Schauer 1995). Nearly all previous work has shown a seasonal decline in reproductive success (e.g. Boekelheide *et al.* 1990; but see Murphy & Schauer 1994; Hipfner & Bryant 1999), usually ascribed to deterioration in food availability, environment, and/or synchronicity. However, a recent series of experimental studies on Brünnich's guillemots has revealed parental quality stratification rather than environmental degradation to be the driving force behind much of the seasonal decline in egg size, chick growth, and replacement laying success (Hipfner 1997; Hipfner *et al.* 1997; Hipfner *et al.* 1999).

Further experimental work in Brünnich's guillemots and razorbills (*Alca torda*) demonstrated enhanced early development of wings in chicks from large eggs

(Hipfner & Gaston 1999b; Hipfner 2000). These two species, and the congeneric common guillemot, employ the 'intermediate' developmental strategy (terminology after Sealy 1973); chicks are fed at the nest site for 15-30 d before leaving for the sea at <30% of adult mass, accompanied by their male parent. Early wing growth can be critical to post-fledging survival, since chicks generally glide from the nest-site to the sea; effective gliding is critical for predator avoidance, and also to enable rapid reunions with parents for protection against intra-specific attacks (Gilchrist & Gaston 1997).

As part of a study of the costs of egg laying in common guillemots, we measured breeding performance in relation to season at a small colony in Alaska, USA. A variety of related work has shown seabirds at this colony to be breeding under relatively poor conditions, with high hormonal stress levels (Kitaysky 1999), low attendance (Zador & Piatt 1998), and low food availability (Robards *et al.* 1999). Reproductive costs may be difficult to identify in average or good conditions, and expressed only in relatively poor conditions or low quality individuals (Stearns 1992); we therefore expected to find relatively strong seasonal effects on breeding performance in this colony. Here we describe the pattern of variation in egg size, hatching success, breeding success, fledging success, and fledging age over the course of the breeding season, and we compare our findings to results from other studies.

Methods

Study area

The study was conducted at the common guillemot colony on Duck Island, Cook Inlet, Alaska (60 09′ N, 152 34′ W) between June-September 1999. Duck Island supports ca. 2500 guillemots in addition to ca. 3000 black-legged kittiwakes *Rissa*

tridactyla, 3000 horned puffins *Fratercula corniculata*, and ca. 500 glaucous-winged gulls *Larus glaucescens* (Piatt *et al.* unpubl. census data). Guillemots breed in two broadly-defined habitat types at Duck Island; cliff areas and inland areas. Cliff areas resemble the 'normal' guillemot breeding habitat, ranging from small ledges on vertical cliff faces to wider platforms on non-vertical rock slopes. The inland areas consist of bare soil at cliff tops, defoliated at the ground level (presumably by excessive acidification from build-up of guillemot guano) but with a variable secondary covering of woody bushes. Nest sites used in this study were distributed across both types of habitat.

Timing and productivity

We monitored the breeding chronology and breeding success of common guillemots following a modified version of the Type 1 protocols detailed by Birkhead and Nettleship (1980). Using digital colour photographs or hand-drawn sketches, we mapped each site where a guillemot was present in the pre-laying period. We then visited plots every fourth day, and recorded the presence and posture (e.g. standing, incubating, brooding) of the nesting adults. The 3 d intervals between visits means that all dates presented in this paper are accurate to within at least 3 d and have error of +/- 2 days; however, we assume the error to be normally distributed and thus not to affect the analyses presented here. We define laying date as the first day we either recorded an adult in an incubating posture or saw an egg at a site where there had not been one on the previous visit. Because guillemots incubate their eggs very tightly, only rarely revealing the egg to observers, it was necessary to infer some egg-laying dates based on first recording of incubating posture at sites where an adult was observed in an incubating posture on at least three consecutive visits (Murphy & Schauer 1996). For those sites that already had an adult in incubating posture or an

egg present when first visited or mapped, we back-calculated laying date from hatch date, using the normal incubation period of 33 d (Birkhead & Nettleship 1987; Gaston & Jones 1998). This method appeared to be reliable, as it correctly forward-predicted hatching date (+/- 2 d) at most sites where laying date was known.

The presence of just-hatched chicks can also be difficult to determine directly. We therefore similarly defined hatching date as the first day we either recorded an adult in brooding posture or saw a chick at a site where there had not been one on the previous visit. Chicks were considered to have 'fledged' if they disappeared >= 15 d at the nest site; any chicks that disappeared prior to age 15 d were assumed to have died. Fledgling age is defined as the inclusive number of days from the hatching date to the day prior to the date when the chick was first recorded as not present.

Hatching success is taken as the proportion of active nest sites (sites where the presence of an egg was either inferred or directly observed) that produced a chick, and reproductive success the proportion of active nest sites that fledged a chick (Birkhead & Nettleship 1980). As documented in other studies of guillemot productivity, we witnessed one female guillemot losing her egg immediately after laying, and noted evidence of egg predation from unknown nests on many other occasions. Thus we can assume that some guillemot pairs laid and lost their egg in the 3 d interval between any two successive observation days, implying that our measurements of both hatching and breeding success represent overestimates (Boekelheide *et al.* 1990); however, because our observation effort was constant during the season, any overestimates should also be constant and should not affect the trends documented here. For those nest sites where the first egg was lost and a second egg was laid, we used the laying date of the first egg in relation to the success of the second egg. We define fledging success as the proportion of nest sites where a chick was present that fledged a chick (Birkhead & Nettleship 1980).

Egg size and quality

To obtain data on egg size in relation to laying date, we carried out daily checks of a separate group of nest sites using similar protocols to those already described. These nest sites were observed from a hide located 1-10 m from ca. 150 inland nest sites. After incubation was confirmed, we used an egg-grabbing tool to remove eggs with known laying dates. The tool was a 'Helping Hand' (designed as a grasping extension for people with limited mobility), modified with padded jaws and attached to a telescoping 8 m fibreglass pole. The claw's trigger was fitted with a trailing line, allowed us to remain concealed while seizing eggs up to 7 m from the hide, minimising colony disturbance. Parental reaction to egg removals varied widely, but the majority of attending parents remained in contact with their nest site during egg-removal bouts, and parental behaviour in the targeted sub-colony normalised after ca. 1 hour. Egg-predating glaucous-winged gulls were kept away from eggs left unprotected during removal activities by judicious use of thrown pebbles or sticks. We measured the length and maximum breadth of each removed egg (+/- 0.1 mm) using callipers. Egg volume indices were calculated using the formula (length*breadth^2; Birkhead & Nettleship 1984).

Fresh eggs were boiled for ca. 12 min within 48 h of collection, placed inside a plastic bag, and stored in a freezer until later analysis of composition. In the laboratory, we weighed each egg, then thawed and separated the eggs into shell, yolk, and albumen. Each component was dried separately at 60°C to constant mass. Components were reweighed to determine dry mass and percent water content. Since nearly all egg lipid is contained in the yolk (Carey 1996), we measured the lipid content of the yolk only. We extracted lipid from the yolk using Soxhlet extraction with petroleum ether as a solvent (Dobush *et al.* 1985). Samples were then dried again

and reweighed, and lipid content determined by subtraction. The boiling and freezing processes altered egg water content, and we therefore present comparisons in dry mass terms only.

Statistical analyses

Statistical analyses were carried out using SPSS (version 7) software. Seasonal trends in hatching success, fledging success, and breeding success were analysed using logistic regression and log-likelihood ratio tests. Linear regression was used to analyse seasonal variation in egg volume, egg mass, and fledging age and condition of young. All tests are two-tailed and considered significant at probability levels less than α=0.05. Means are given $\pm$ 1 SE.

Results

The pattern of egg laying at Duck Island in 1999 was unimodal and moderately skewed to the left (Fig. 1). The middle 80% of females laid within 18 days, and the median date of egg-laying was 15 July, well within the normal range of median laying dates over the previous four years of study at Duck Island (4 July to 23 July; Piatt *et al.* unpubl. data). The variation in laying dates, as expressed by the Coefficient of Variation (CV), was 49.6%.

Egg size and quality

The mean volume index of first eggs at Duck Island was 216.00 ± 2.34 (n=52), at the upper end of the range of sizes reported at other colonies (Table 1). The sizes of first eggs varied considerably. There was no significant relationship between first egg volume and laying date (Fig. 2). However, the dry mass of first eggs was

Figure 1. The timing of egg laying at Duck Island, Alaska, in 1999. All laying dates known to within +/- 2 d are included, in 4 d groups.

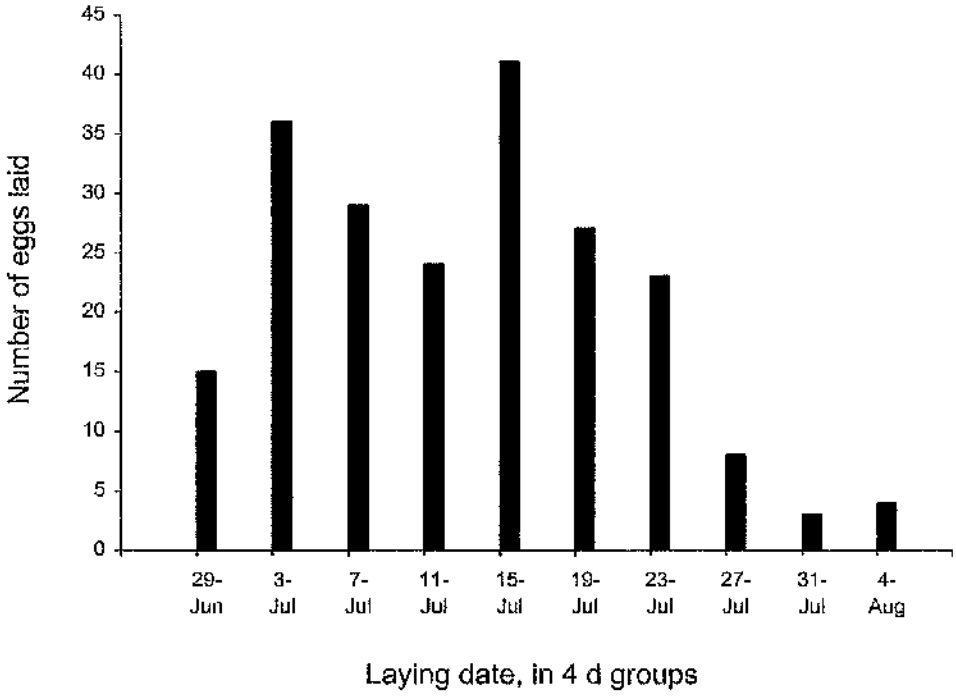

Number of eggs laid
45
40
35
30
25
20
15
10
5
0
29-Jun
3-Jul
7-Jul
11-Jul
15-Jul
19-Jul
23-Jul
27-Jul
31-Jul
4-Aug
Laying date, in 4 d groups

Table 1. Volume indices reported for common guillemot eggs at selected colonies.

Source	Year	Location	Mean volume index	SD	N
This study	1999	Duck Island, Alaska	216.00	16.9	52
Hatchwell and Pellat 1990	1987	Skomer Island, Wales	204.80	10.5	20
Hatchwell and Pellat 1990	1986	Skomer Island, Wales	199.27	11.1	20
Birkhead and Nettleship 1987	1981	Gannet Islands, Labrador	218.60	18.7	198
Birkhead and Nettleship 1987	1982	Gannet Islands, Labrador	218.90	19.5	217
Birkhead and Nettleship 1987	1983	Gannet Islands, Labrador	215.30	20	250

significantly related to laying date (Fig. 3), with later-laid eggs having a lower dry mass.

Breeding success

Overall mean hatching, fledging, and reproductive success values are shown in Table 2. Logistic regressions showed highly significant seasonal declines in fledging and reproductive success, but no significant seasonal change in hatching success (Table 2). To further investigate the effects of laying date on within-year breeding success, we followed the convention introduced by Murphy and Schauer (1994), dividing frequency distributions of laying dates of first eggs in quartiles, and then examining the relationships of breeding success parameters to grouped laying dates (Table 3). There were no significant differences between groups, indicating that the seasonal declines in success expressed using logistic regressions were gradual and not severe enough to drive differences between mean success of the earliest and latest breeders (Table 3).

Fledging age and condition

Based on observations of chicks of fledging age disappearing from productivity plots, the fledging age declined over the season (Fig. 4). A similar decline in estimated age was found in fledglings captured en route to the sea (Fig. 5). The slopes of the linear regressions suggest an average reduction in fledging age from roughly 22 d for chicks from the earliest eggs to 18 d for chicks from the latest eggs over the month-long fledging period. Fledglings were captured over a 16 d period; there was no relationship between date of capture and body condition (Fig. 6).

Figure 2. Volume indices of common guillemot first eggs in relation to laying date, at Duck Island, Alaska, in 1999. There was no relationship between volume index and laying date.

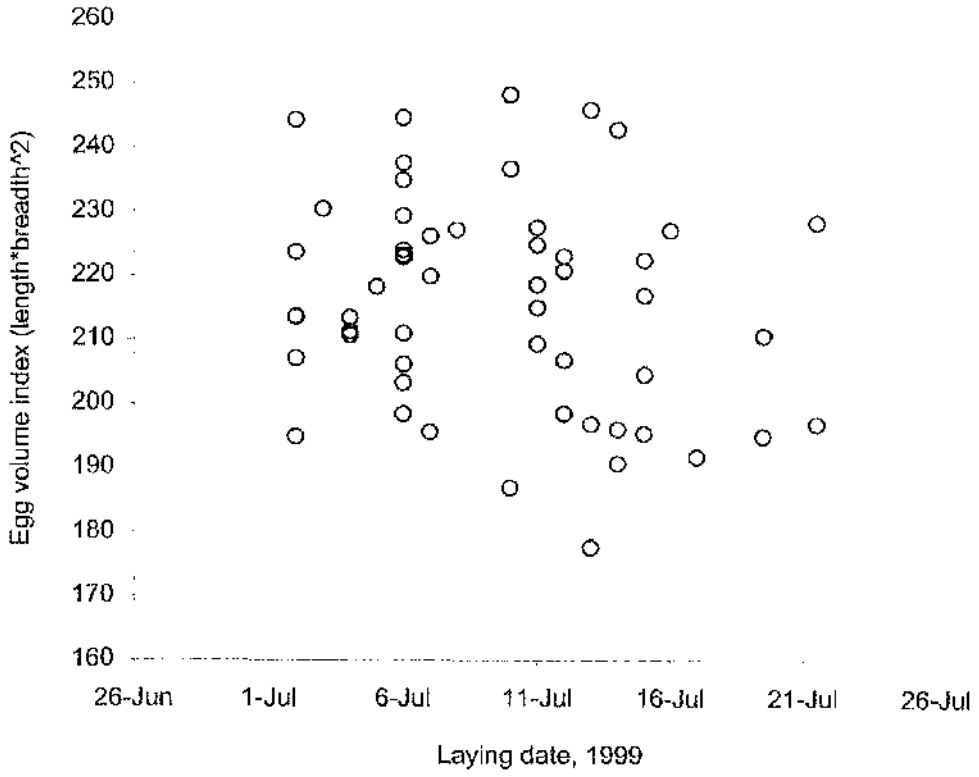

260
250
240
230
220
210
200
190
180
170
160
Egg volume index (length*breadth^2)
26-Jun
1-Jul
6-Jul
11-Jul
16-Jul
21-Jul
26-Jul
Laying date, 1999

Fig. 2

Figure 3. Dry mass of common guillemot first eggs in relation to laying date, at Duck Island, Alaska, in 1999. First egg dry mass declines significantly with laying date (r^2 = 0.242; $F_{1,34}$ = 10.553; P = 0.003).

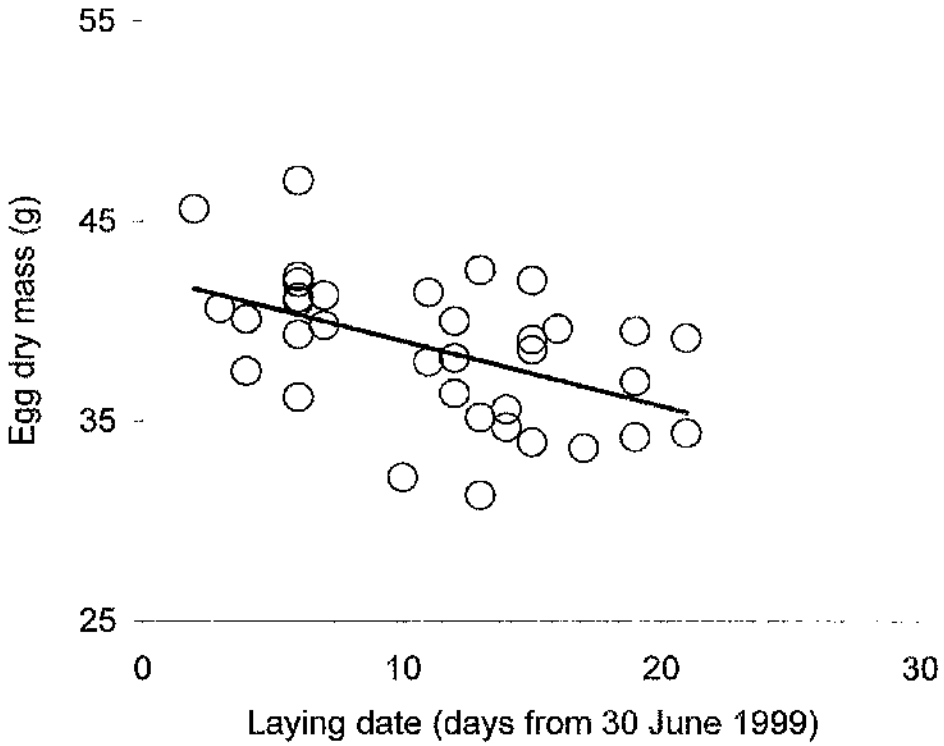

55
45
35
25
Egg dry mass (g)
0
10
20
30
Laying date (days from 30 June 1999)

Table 2. Logistic regressions showing significant seasonal trends in common guillemot fledging and reproductive success at Duck Island, Alaska, in 1999. Hatching, fledging, and reproductive success (hatched or not; fledged or not; egg gave rise to a fledgling or not) were entered as dependent binary response variables, with laying date (relative to 30 June) as the covariate.

Parameter	Hatching success	Fledging success	Reproductive success
n =	132	110	132
success	0.83 ± 0.03	0.77 ± 0.04	0.64 ± 0.04
Wald	0.77	8.50	9.10
P =	0.38	0.0035	0.0026
Slope	-0.025	-0.088	-0.075

Table 3. The effects of laying date on guillemot breeding success at Duck Island, Alaska, in 1999. Laying dates are grouped into three categories: the first quartile (Early), the middle two quartiles (Middle), and the fourth quartile (Late). Hatching, fledging, and reproductive success are compared across the three categories using Chi-square contingency tables, with Yates' correction applied. All test were non-significant, with two degrees of freedom.

	Hatched		**Fledged**		**Reproduced**	
Phase	**Yes**	**No**	**Yes**	**No**	**Yes**	**No**
Early	22	2	20	3	20	4
Middle	57	13	45	12	45	25
Late	30	8	20	10	20	18
χ^2	0.961		2.124		4.800	
P	$\cong 0.60$		$\cong 0.37$		$\cong 0.09$	

Figure 4. The relationship between fledging age and laying date among common guillemots at Duck Island, Alaska, in 1999, determined through observations of nest sites in productivity plots. Fledging age has a significant negative correlation with laying date ($y = 22.211 - 0.134x$; $r^2 = 0.06$; $F_{1,80} = 5.271$; $P = 0.024$).

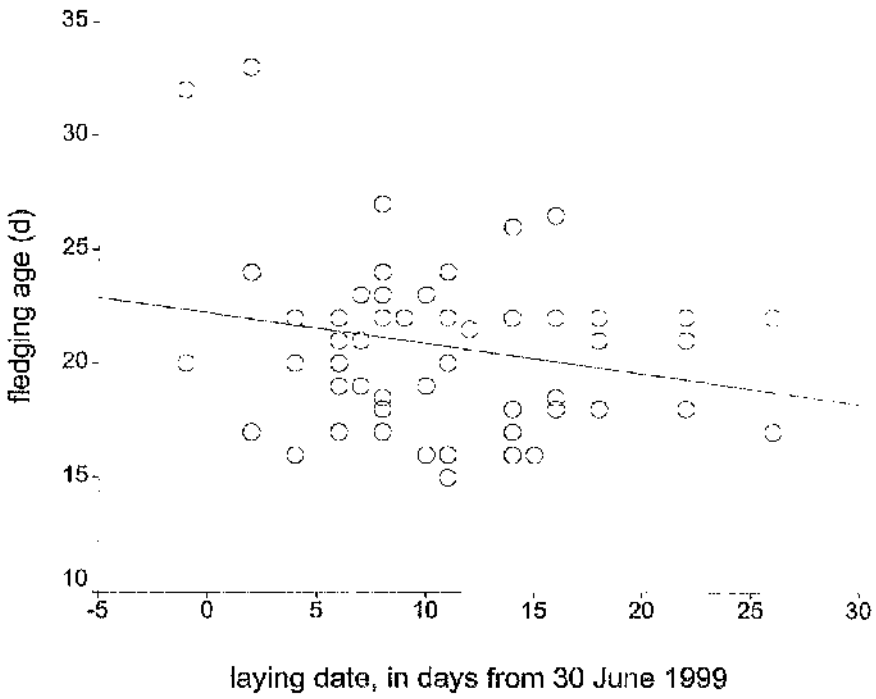

fledging age (d)
35
30
25
20
15
10
-5
0
5
10
15
20
25
30
laying date, in days from 30 June 1999

Figure 5. The relationship between estimated fledging age and capture date of common guillemot fledglings captured on their way to the sea at Duck Island, Alaska, in 1999. Estimated age is from wing length-age correlation determined in a related study at Duck Island in 1999 (see Chapter 4). Fledging age is negatively correlated with capture date ($y = 25.988 - 0.268x$; $r^2 = 0.07$; $F_{1,90} = 6.978$; $P = 0.010$).

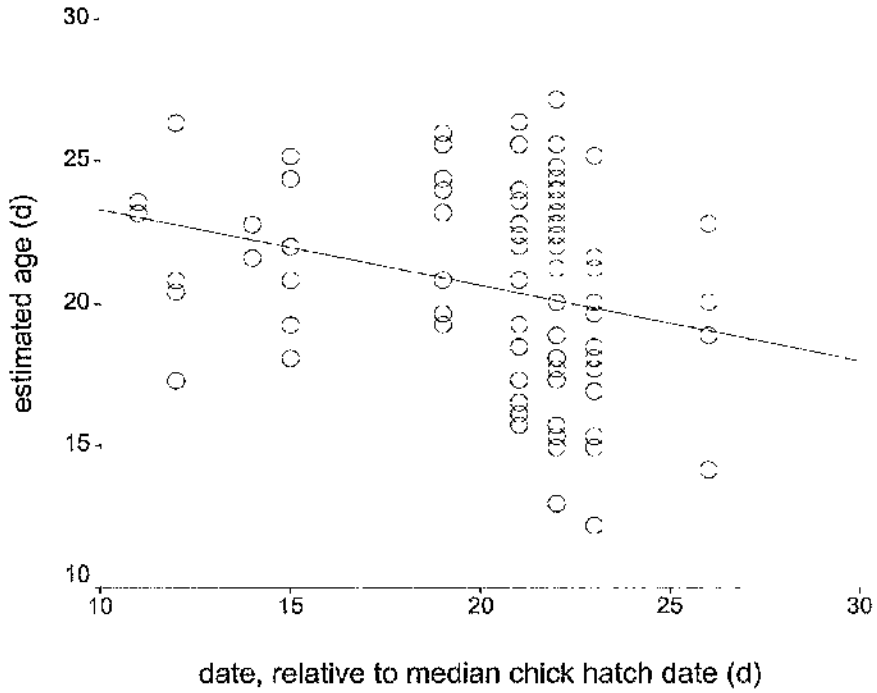
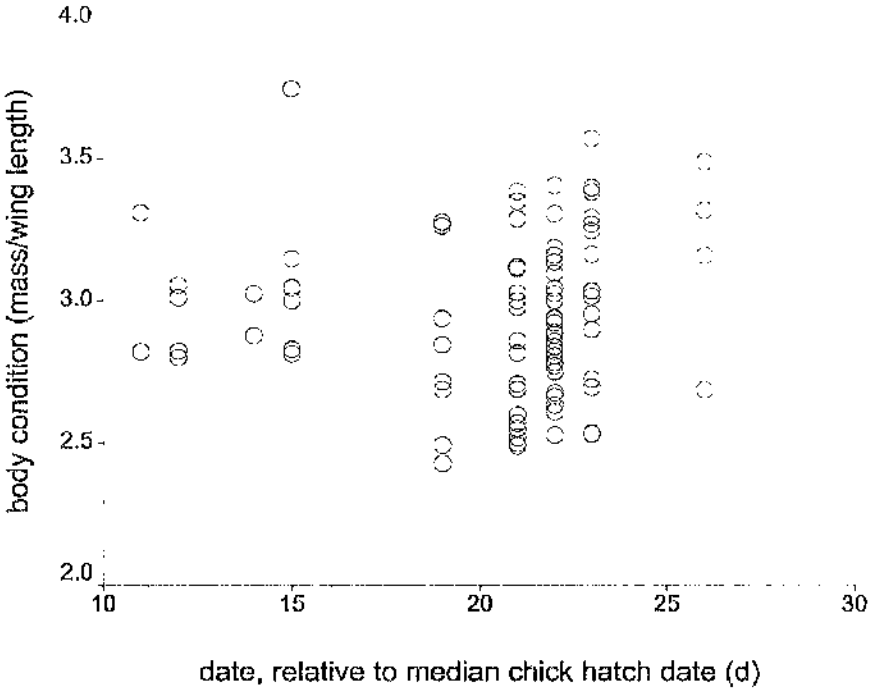

30
25
20
15
10
estimated age (d)
10
15
20
25
30
date, relative to median chick hatch date (d)

Figure 6. The relationship between body condition and capture date of common guillemot fledglings captured on their way to the sea at Duck Island, Alaska, in 1999. Capture date did not explain any of the variation in fledgling body condition (r^2 = 0.00; $F_{1,90}$ = 0.012; P = 0.913).


4.0
3.5
3.0
2.5
2.0
body condition (mass/wing length)
10
15
20
25
30
date, relative to median chick hatch date (d)

Discussion

The seasonal pattern of guillemot egg laying at Duck Island during 1999 was roughly unimodal and not dramatically skewed in either direction. This laying pattern was divergent from the typically skewed pattern in this species of an early sharp increase in laying to a peak, followed by rapid taper to low levels of laying that are sustained for a variable duration (Birkhead & Nettleship 1987; Boekelheide *et al.* 1990). The middle 80% of females laid over an 18 d period, representing a low though not exceptional degree of synchrony relative to other published guillemot studies. Over three years of study in Labrador, Birkhead & Nettleship (1987) found that the middle 80% of females laid over a mean of 8 days (range 6-10). Working on Skomer Island, Wales, Birkhead found the laying period of the middle 80% of eggs to vary between 9-20 days (Birkhead 1980) and 13-14 days (Hatchwell 1991). At Skomer Island, the laying synchrony was shown to positively relate to breeding density, with high nest density areas exhibiting high synchrony and consequent higher productivity (Hatchwell 1991). We made no measures of density in our study areas, and are thus unable to analyse variance in egg-laying at levels other than whole-colony.

The relatively low egg laying synchrony at Duck Island may be an indicator of relatively high early egg predation. The colony population has declined dramatically over the last two decades, with numbers remaining stable but low over the last five years. The population may thus currently represent some baseline population level, with minimal group-defence protection against the abundant egg predators present at the colony during the egg-laying phase. The sub-colonies may be less able to synchronously swamp egg predators, resulting in many eggs being taken early and a consequently greater spread of first and replacement egg-laying.

Breeding success

Despite poor breeding conditions, the hatching, breeding, and fledging success of guillemots at Duck Island were all within typical levels reported for the species at other colonies (Piatt & Van Pelt unpubl. data; review in Murphy & Schauer 1994; Gaston & Jones 1998). This is consistent with past work showing guillemots to exhibit relatively consistent breeding performance across a wide range of moderate to good food availability, with much lower coefficients of variation in breeding success than coexisting species such as kittiwakes or cormorants (Boekelheide *et al.* 1990; Uttley *et al.* 1994). Guillemot breeding consistency is thought to result from their ability to buffer against changing feeding conditions by changing the amount of time they spend foraging (Burger & Piatt 1990; Piatt & Anderson 1996).

However, as expected, we did find seasonal declines in reproductive parameters. Fledging success and reproductive success showed significant declines across the season, with chicks fledging from 83% of early nests versus only 53% of late nests. Interestingly, the mechanism by which this decline operated contrasted to the seasonal declines previously reported in this species; hatching success was very high and did not decline over the season (Table 2, 3; mean 83%; compare to range 60-85% reviewed in Murphy & Schauer 1994) while fledging success was moderate, driving down the mean reproductive success to a relatively low level (Table 2, 3; mean RS 64%; compare to range 53-83% in Murphy & Schauer 1994). The one-egg clutch of marine birds such as guillemots has been proposed as an adaptation for sustainable chick provisioning under the extremely demanding conditions of capturing patchy, distant prey (Lack 1968). However, most guillemot studies have found differential breeding success to occur more at the egg than the chick stage (e.g. Wanless & Harris 1988), and recent work in the Laridae has demonstrated a within-season trade-off

between egg production and chick provisioning, revealing egg production to be a significant factor in the investment decisions made by breeding birds (Monaghan *et al.* 1998). In the current study, we have no information on seasonal variation in prey abundance; it is possible that food availability worsened over the season. The constraints of brooding and provisioning also could affect the ability of parents to obtain prey, further driving the relatively low fledging success at this colony.

Egg size and quality

First egg volumes at Duck Island were within the range of first egg volumes measured at other guillemot colonies in North America and Britain (Table 1). We found no relationship between season and egg size, in contrast to previous work that has shown a seasonal decline in egg volume (Birkhead & Nettleship 1982). However, we did find a significant decline in first egg dry mass as the breeding season progressed (Fig. 3); we consider dry mass a more accurate measure of egg quality than size, since the relative nutrient content of eggs has been shown to change independent of egg volume and is linked to the probability of the egg giving rise to a fledged chick (Nager *et al.* 2000). Egg quality also declined across the season (see Table 1, Chapter Five). Based on the finding that a larger egg translates into a hatchling with larger yolk reserves but not a larger skeleton, and that chick growth rate exceeds egg formation rate, it has been hypothesised that the seasonal decline in egg size in auks is an adaptive response to progressively worsening feeding conditions (or other environmental limitation, e.g. shortage of chick-rearing time due to onset of freezing conditions) over the breeding season, allowing late parents to produce a small egg earlier instead of further delaying breeding to produce a larger egg (Birkhead & Nettleship 1982).

Fledging age and condition

Chicks growing from eggs laid later in the breeding season tended to leave our study colony at a younger age, as has been widely reported for guillemots at other colonies (e.g. Gaston & Nettleship 1981; Birkhead & Nettleship 1982; Birkhead & Nettleship 1987; Wanless & Harris 1988; Boekelheide *et al.* 1990; Hatchwell 1991; but also see Hedgren & Linnman 1979). A variety of explanations has been proposed to account for this trend, based on a progressive seasonal change in the costs and benefits of staying at the colony versus departing to sea. Increased costs of remaining at the colony include decreasing local food availability and increasing predation risk (Wanless & Harris 1998). However, there are limits to early departure; sufficient growth of wing feathers to allow controlled gliding and diving has been proposed as the key factor determining immediate survival of fledglings (Hipfner & Gaston 1999b).

In a recent review, Moreno (1998) evaluated four hypotheses explaining seasonal declines in breeding success of seabirds: i) food availability decreases throughout the season, ii) late nests suffer increased predation, iii) young or inexperienced breeders breed late, and iv) late breeders do not invest as much in their breeding attempt as early breeders. While acknowledging the probable importance of changes in food availability and of the reduction in predation provided by local synchrony, Moreno concludes that available experimental evidence does not support the parental quality hypothesis, and proposes that the 'restraint' hypothesis is the most plausible (Moreno 1998). Experimental work in the great tit has supported the 'date' hypothesis (changing environment affecting all individuals) over the parental quality hypothesis (Verhulst *et al.* 1995; Verboven & Verhulst, 1996). However, Daunt

et al. (1999) have demonstrated age-related differences in reproductive performance independent of changes in the environment. Further experimental work may more clearly resolve the relative influences of these non-exclusive hypotheses in seasonal trends in reproductive success.

We expected to find relatively strong seasonal declines in breeding performance at this declining, apparently food-poor, colony. Our results do provide evidence for seasonal declines in success, egg quality, and fledging age- but the trends were not exceptionally strong. The fact that no seasonal trend in hatching success or in chick condition at fledging was observed suggests some influence of individual quality or of a threshold effect whereby some pairs abandoned their offspring, but remaining pairs were able to provision their chicks at a rate sufficient to produce fledglings of equal condition to those produced earlier in the season. Other variables such as predation or decreasing synchrony were not measured, but could also have been important in driving the observed seasonal declines.

Chapter Four

The relationship between productivity and body condition in adult and fledgling common guillemots *Uria aalge*

The data from Duck Island presented in this chapter were collected by myself, with help from Ann Harding. The data from Gull Island were collected by Mike Shultz (USGS) and field assistants. I conducted all analyses and wrote the manuscript.

Introduction

That reproduction carries costs is a central tenet of life history theory, underpinning the concept of an adjustable parental effort that balances reproductive investment and survival (Drent and Daan 1980; Stearns 1992; Pettifor 1993). Reproductive performance generally varies within and between populations (Drent and Daan 1980), due to biological differences between individuals and to temporal and spatial heterogeneity in the environments they experience. However, defining the links between these sources of variation and their expression in reproductive performance has proven difficult, despite interest in their utility as tools to help understand fluctuations in productivity among natural populations.

In birds, the most common approach has been to simultaneously measure reproductive performance and (if possible) effort in conjunction with parental body condition. Adult body condition has been used as the 'currency' of reproductive trade-offs in a large number of experimental studies (Bryant 1988; see Golet *et al.* 1998 for review). In those experimental studies that involved adults rearing enlarged broods, roughly half have shown a negative effect on parental body condition, with the equivocal results of the remainder often being explained by the suggestion that costs are only detectable in extreme situations, beyond some threshold that varies with species and situation (De Steven 1980; Wernham and Bryant 1998). As an alternative to experimental work, other studies have drawn correlative links between food supply, productivity, and parental body condition as a currency of effort (Drent and Daan 1980; Monaghan *et al.* 1989; Hamer *et al.* 1993). While evidence for the correlation between food supply and reproductive success is widespread (Martin 1987; Monaghan *et al.* 1989; Harris and Wanless 1990; Uttley *et al.* 1994; Monaghan *et al.* 1996), there has emerged no consistent relationship between reproductive demand

(whether natural variation in food availability or experimental alteration), productivity, and parental effort, and it is likely that any optimal balance between these factors will vary in a complex manner between species, sexes, and local situations (Martin 1995; Monaghan *et al.* 1998).

In this study we report on measures of reproductive success and body condition in adult and fledgling common guillemots (*Uria aalge*) at two small colonies in Alaska characterised by markedly different prey habitats and foraging ranges (Robards *et al.* 1999; Piatt *et al.* unpubl. data). Guillemot breeding performance appears to be buffered against a wide range of differences in food availability, and reproductive success is not normally closely linked to variation in food supply (Piatt and Anderson 1996). However, productivity can be sharply reduced or entire colonies may fail to breed in years of extremely poor food supply. Variation in the condition of chicks at fledging has been ascribed to both variation in food availability (Gaston & Nettleship 1981) and other colony-specific factors such as colony size (Gaston *et al.* 1983). We examine the relationship between variation in productivity and body condition of both adults and fledglings, between two years and two colonies, taking advantage of colony-years with extremely poor and extremely good productivity to maximise the chance of detecting effects. Since the relationship between adult condition and reproductive performance may be masked by colony-specific or other local factors, we made the following comparisons: two years of contrasting productivity at the same colony, and two colonies with contrasting productivity in the same year. We addressed three questions: 1) how is productivity related to adult body condition, 2) are negative effects of body condition more likely to be expressed in females due to the concentrated and inflexible costs of egg production, and 3) how are adult condition, productivity, and offspring condition linked? An evaluation of the data in relation to these questions should provide insight into the strength of links between

variation in productivity, environment, and parental costs, and may also contribute to increasing the sensitivity of guillemot population monitoring schemes (Monaghan 1996).

Methods

Study location and background

The common guillemot is a highly colonial seabird with a circumpolar boreal and low-Arctic distribution. Only one egg is laid (although lost eggs may be replaced; Chapter Five) and both sexes share incubation and chick provisioning. The chick is fed at the nest for 15-30 days; leaves the colony at < 30% of adult mass, and is subsequently cared for by its male parent for up to six weeks.

Our work was conducted at two common guillemot colonies in Cook Inlet, Alaska between June-September in 1998-1999. The colony at Duck Island (west side of Cook Inlet; 60° 09′ N, 152° 34′ W) currently supports ca. 2500 guillemots, representing a steady decline to ca. 10-20% of maximum counts made in the early 1970s, while the Gull Island colony (east side of Cook Inlet; 59° 35′ N, 151° 19′ W) has expanded over the same time period, and currently supports ca. 5000 guillemots. The two colonies are separated by 100 km and are in oceanographically distinct habitats (Robards *et al.* 1999). A number of independent measures made concurrently with this study (nearshore forage fish abundance; offshore midwater fish availability; adult foraging trip duration and 'loafing' time at the nest; stress hormone levels) provide strong evidence that guillemots breeding at Duck Island experienced food shortages during the 1995-1999 breeding seasons and are relatively highly stressed, while guillemots breeding at Gull Island experienced relatively greater prey availability and lower stress (Kitaysky *et al.* 1999; Robards *et al.* 1999; Zador & Piatt

1999; J.F. Piatt *et al.*, unpublished data). Furthermore, at-sea surveys show that birds breeding at Duck Island must travel further to access prey (Piatt *et al.* unpubl. data). However, over five years of study (1995-1999), the reproductive success of guillemots at Gull Island has been lower, on average, than that of guillemots at Duck Island (Piatt *et al.* unpubl. data).

We monitored the breeding chronology and success of guillemots in study plots following a modified version of the Type 1 observational methods detailed by Birkhead & Nettleship (1980); full details of methods used to calculate parameters of reproductive success are given elsewhere (Chapter Two). Briefly, hatching success is taken as the proportion of eggs hatching, fledging success the proportion of hatched chicks that fledged, and reproductive success the proportion of nest sites where an egg was laid from which a chick fledged (Birkhead & Nettleship 1980). After colony departure, chicks continue to be cared for by the male parent for up to two months (Varoujean *et al.* 1979), but for convenience here, and in accordance with previous studies on this species, we define chick departure from the nest site as 'fledging', and chicks that have departed the nest site as 'fledglings'. Since 15 days is the minimum nest departure age in common guillemots (Gaston & Jones 1998), chicks were considered to have 'fledged' successfully if they disappeared from the nest site >= 15 d after hatching; any chicks that disappeared prior to this were assumed to have died. Fledging age is taken as the inclusive number of days from the hatching date to the day prior to the date when the chick was first recorded as not present.

Adult condition

We captured breeding adults at intervals throughout the season, using a telescoping fibreglass pole fitted with a noose. A few birds were recaptured over the course of the study, but we targeted birds that had not previously been ringed, and use only

first captures for this analysis to ensure independence of the samples. All birds captured were actively attending a nest site, egg, or chick. Captured birds were ringed with a unique combination of colour rings and a metal USFWS ring, and a small blood sample for sex determination was taken from the wing. Blood was collected and stored in a 1.8 ml vial that had been pre-filled with a buffering solution. The sex of the bird was later identified from red blood cell DNA, using two *CHD* genes (Griffiths *et al.* 1996). We measured body mass ± 5 g using spring scales; head-plus-bill and tarsus length ± 1 mm using vernier callipers; and flattened standard wing length ± 1 mm ('elbow' [carpus] to distal end of longest primary feather) using a stopped ruler.

To obtain an index of body size for adults, we performed a principal components analysis (PCA) on the linear measurements of all captured adults (n = 474; Freeman & Jackson 1990). The resulting coefficients had consistent loadings (head-plus-bill 0.544, tarsus 0.579, wing 0.607), and the first principal component accounted for 54% of the variance in the original measures. Measurement data were multiplied by the coefficients, and added together to produce a PCA factor score for each adult, hereafter called the 'body size index'. Mass was then plotted against the body size index; the resulting least-squares regression equation predicts mass for an adult of a given size. We used residuals from this regression (expressed as a percentage by which a bird's actual mass differs from predicted mass) as an index of individual adult condition (hereafter called 'body condition'; Golet & Irons 1999; Jakob *et al.* 1996).

For analysis, capture dates were standardised relative to the median chick hatching date (MCHD) of each year, and grouped into three phases of breeding: Prelaying (>32 d prior to MCHD); Incubation (between -32 d and MCHD); and Chick rearing (dates greater than MCHD).

Fledgling condition

We captured fledglings as they made their way across cliff-base rocks toward the ocean. Captures were timed to overlap with the peak in numbers of fledglings. We measured mass ± 1 g using a spring scale, and flattened standard wing length ± 1 mm (from the carpus to tip of the longest feather). Processing each fledgling generally took no longer than 1 minute, and fledgling behaviour post-handling appeared to be no different from fledglings that were not captured.

Age of fledglings was estimated using a wing length-age regression determined from known-age chicks in a separate study at Duck Island (Chapter Five). Using body size to estimate offspring age can be imprecise (Cooch *et al.* 1999); we therefore compared estimated ages with ages determined by chick departure from nest-sites in observed plots. Ages did not differ (see fig. 6, 7) and we therefore assume that captured fledglings comprise a representative sample. We express fledgling body condition as a size-corrected index by dividing mass by wing length, hereafter called 'body condition'.

Ethical note

All captures were carried out under the authority of permits issued by the US Fish and Wildlife Service and the Alaska Department of Fish and Game. Handling times were minimised wherever possible to reduce the stress of capture.

Statistical analyses

We compared adult condition in relation to sex, colony, and year using two- and three-way ANOVAs; where significant effects were found, we used Sheffé's multiple comparison tests. The relationships between fledgling wing length and mass were

compared between colonies and years using ANCOVA. We used *t*-tests to compare fledgling means between colonies and years, after ensuring that the assumptions of approximate normality were met and assuming equal or unequal variances as appropriate. Analyses were carried out using SPSS; all tests are two-tailed and considered significant at probability levels less than $\alpha = 0.05$. Means are given $\pm$ 1 SE.

Results

Reproductive success

Hatching success, fledging success, and overall reproductive success were all higher at Duck Island in 1999 than either Duck Island in 1998, or Gull Island in 1999 (Table 1). Thus it is possible to make the following comparisons: i) an intra-colony comparison at Duck Island between a year characterised by near-failure of breeding (1998) and a year of relatively high productivity (1999), and ii) an inter-colony comparison within 1999 between two colonies experiencing low productivity (Gull Island) and high productivity (Duck Island)

Adult body condition

We regressed body mass on body size indices of all captured adults, generating separate linear regressions for female, male, and unknown-sex adults (Fig. 1). The relationship between size and mass did not differ between these groups (Fig. 1), and we therefore pooled all data. However, we did include sex as a factor in some analyses to check for any differences between males and females at particular phases. We detected no significant effect of sex on body condition in either year or at either colony (Fig. 2, 3).

Table 1. Measures of common guillemot reproductive performance at two colonies in lower Cook Inlet, Alaska. Results of *t*-tests between years (Duck Island 1998 to 1999) and colonies (1999 Duck Island to Gull Island) are shown between the compared parameters, with significant differences in **bold**.

Year	1998		1999		1999
Colony	Duck		Duck		Gull
		P		*P*	
Hatching success	0.37 ± 0.26	**<0.001**	0.83 ± 0.15	**0.001**	0.38 ± 0.18
		$t_{17} = -4.466$		$t_{11} = 4.886$	
Fledging success	0.21 ± 0.32	**0.007**	0.70 ± 0.34	~0.2	0.44 ± 0.33
		$t_{16} = -3.141$		$t_{11} = 1.356$	
Reproductive success	0.13 ± 0.24	**0.002**	0.63 ± 0.34	**~0.034**	0.21 ± 0.23
		$t_{16} = -3.659$		$t_{11} = 2.418$	

Figure 1. The relationship between body size and mass for all captured adults, grouped as female, male, and unknown. Separate regressions for each group were highly significant (female $r^2 = 0.143$, $F_{1,137} = 22.85$, $P < 0.001$; male $r^2 = 0.132$, $F_{1,163} = 24.75$, $P < 0.001$, unknown $r^2 = 0.158$, $F_{1,166} = 31.351$, $P < 0.001$), but did not differ from each other in slopes (ANCOVA $F_{2,466} = 0.035$, $P = 0.965$) or elevations (ANCOVA $F_{1,468} = 2.785$, $P = 0.064$). The least-squares regression of all data pooled is a significant predictor of the size-specific mean body mass of an individual in the study population ($y = 1042.66 + 23.52x$, $r^2 = 0.155$, $F_{1,470} = 86.731$, $P < 0.001$).

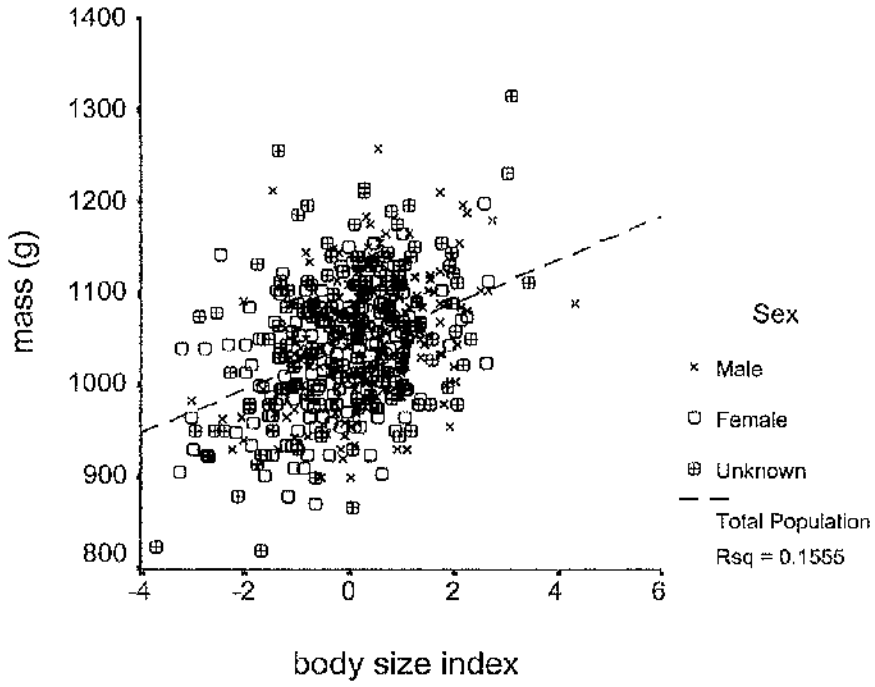
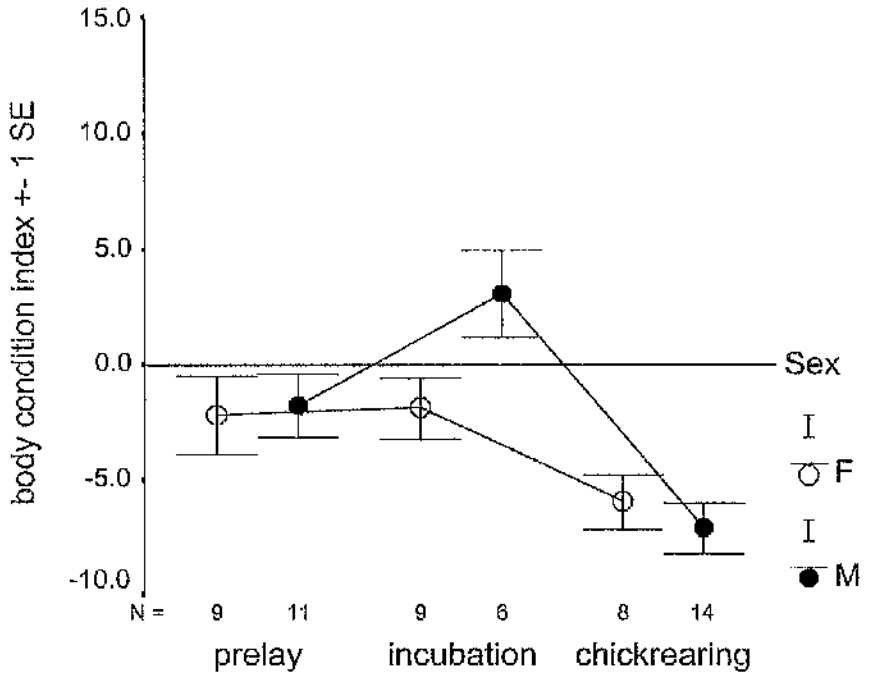

1400
1300
1200
1100
1000
900
800
mass (g)
-4
-2
0
2
4
6
body size index
Sex
Male
Female
Unknown
Total Population
Rsq = 0.1555

Figure 2. Seasonal pattern of the mean body condition of captured adults at Duck Island in 1998 (top panel) and 1999 (bottom panel) by phase of breeding. Filled circles are males; open circles, females. Entering year, sex, and phase as factors in a three-way ANOVA revealed a significant effect of breeding phase on condition; neither sex nor year, nor any of the interaction terms, significantly affected body condition (GLM: phase, $F_{2,129} = 15.336$, $P < 0.001$; sex, $F_{1,129} = 1.334$, $P = 0.250$; year, $F_{1,129} = 0.055$, $P = 0.815$; all interactions $P > 0.20$).

Duck Island 1998



Duck Island 1999

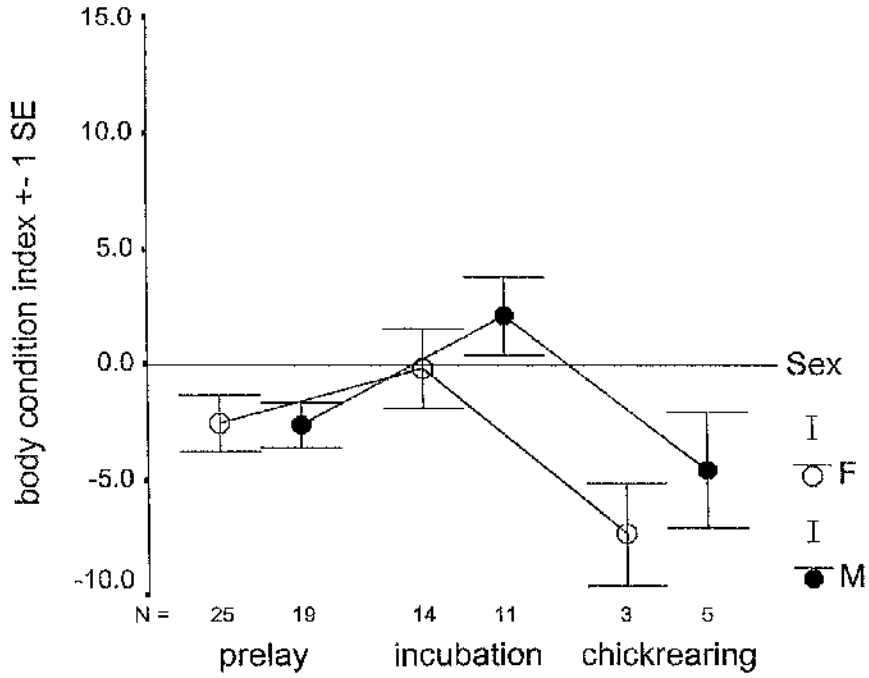
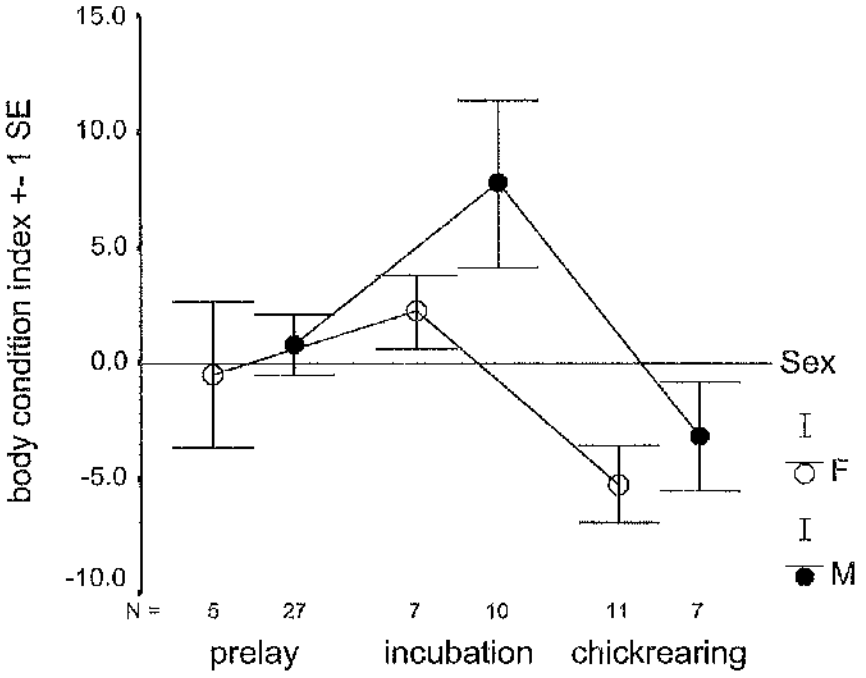
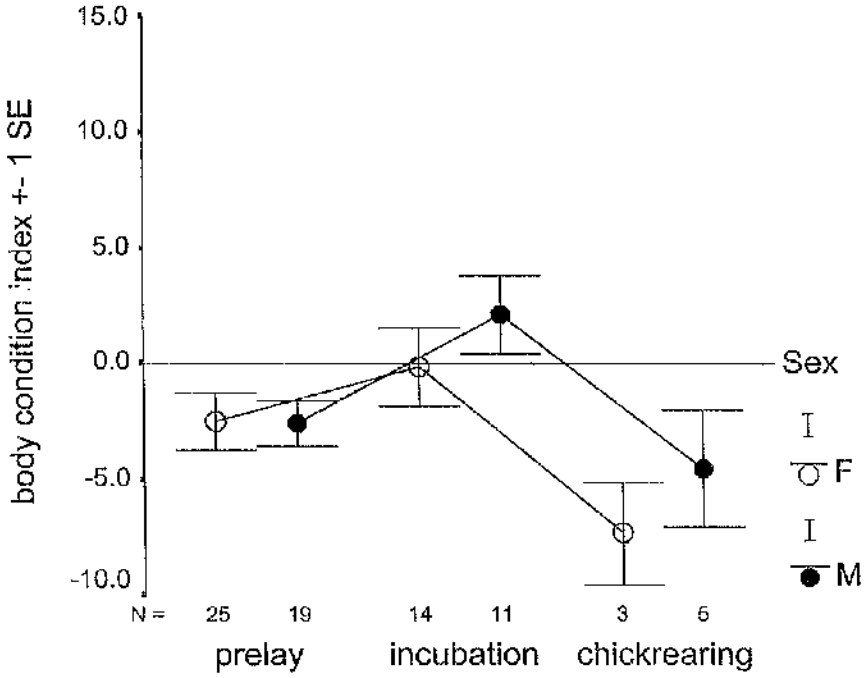


Figure 3. Seasonal pattern of the mean body condition of captured adults at Gull Island (top panel) and Duck Island (bottom panel) in 1999, plotted by breeding phase. Filled circles are males; open circles, females. Entering colony, sex, and phase as factors in a three-way ANOVA showed a strongly significant effect of phase on body condition, and a weaker but still significant effect of colony (GLM: phase, $F_{2,139}$ = 13.739, $P < 0.001$; colony, $F_{1,139}$ = 6.684, $P = 0.011$). Sex did not influence body condition, and none of the interaction terms were significant (GLM: sex, $F_{1,139}$ = 2.588, $P = 0.110$; all interactions $P > 0.40$).

Gull Island 1999



Duck Island 1999



Between-year effects- After pooling the female, male, and unknown-sex adults, we found strong effects of breeding phase on body condition in both 1998 and 1999 at Duck Island. Mean body condition increased from prelaying to incubation, then decreased from incubation to chick-rearing to lower values than during prelaying (Fig. 4). Mean body condition did not change between years, nor did the pattern of body condition in relation to phase (Fig. 4).

Between-colony effects- Strong effects of breeding phase on body condition were also evident among adults breeding at Gull Island and at Duck Island in 1999, with a similar pattern at both colonies (Fig. 5). However, there was also a strong effect of colony on mean condition, with adults at Gull Island being in consistently better condition (Fig. 5).

Fledgling age and condition

Between-year effects- Chicks fledging at Duck Island in 1998 and 1999 appeared to be very similar in all parameters measured; we detected no differences in wing length, mass, condition, or age (Fig. 6). Chick growth between hatching and 15 d was not measured, but between 15 d and fledging there was no detectable difference in the relative rate of structural growth (using wing length as a proxy) and mass gain between years (Fig. 7).

Between-colony effects- Chicks fledging at Gull Island in 1999 tended to be smaller and younger than chicks fledging at Duck Island in the same year, but this difference was not significant (Fig. 8). However, fledglings at Gull Island were significantly heavier than fledglings at Duck Island. This difference became more pronounced when put in terms of body condition, since the slightly smaller structural size of the Gull Island fledglings amplifies the mass difference (Fig. 8). The effect was supported by examining the relationship between wing length and mass (Fig. 9), which shows that

the relative rates of structural growth and mass gain did not differ between colonies, but fledglings from Gull Island of any given size were heavier than those from Duck Island.

Figure 4. Seasonal pattern of the mean body condition of captured adults at Duck Island in 1998 and 1999, with female, male, and unknown sexes pooled. Filled circles are 1999; open circles, 1998. Year and phase were entered as fixed factors in a two-way ANOVA. Condition was strongly affected by breeding phase, increasing with marginal significance between prelay and incubation, then decreasing between incubation and chickrearing (GLM: phase, $F_{2,134} = 15.533$, $P < 0.001$; Sheffé multiple comparisons prelay to incubation $P = 0.037$, prelay to chickrearing $P = 0.001$, incubation to chickrearing $P < 0.001$). Year did not influence condition, and the effect of phase on condition was the same in both years (GLM: phase, $F_{2,134} = 15.533$, $P < 0.001$; year, $F_{1,134} = 0.004$, $P = 0.948$; year and phase interaction, $F_{2,132} = 0.494$, $P = 0.611$).

Duck Island

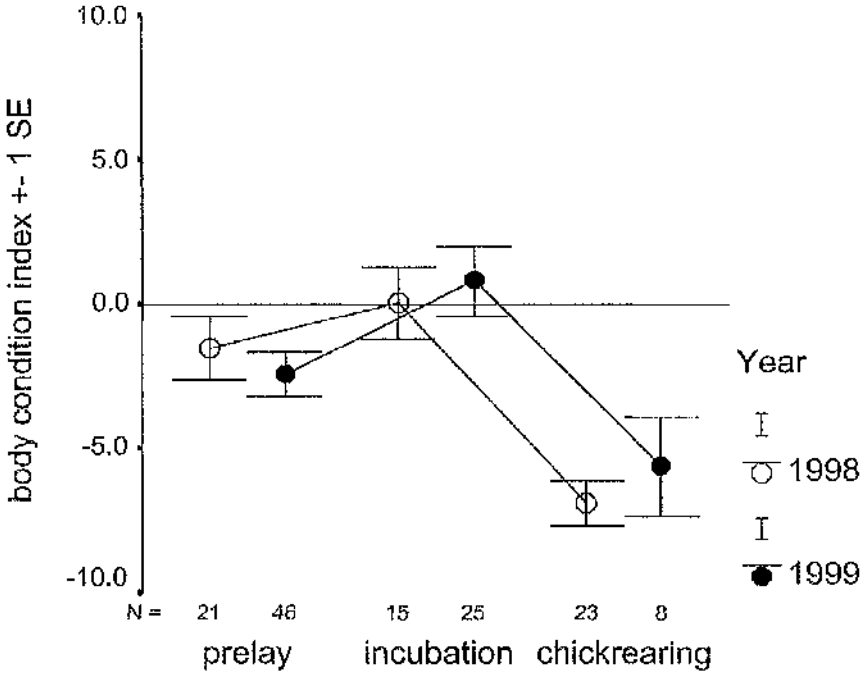

10.0
5.0
0.0
-5.0
-10.0
body condition index +- 1 SE
Year
1998
1999
N = 21 46 15 25 23 8
prelay
incubation
chickrearing

Figure 5. Seasonal pattern of the mean body condition of captured adults at Duck and Gull Islands in 1999, with female, male, and unknown sexes pooled. Filled circles are Gull Island; open circles, Duck Island. Phase and colony were entered as fixed factors in a two-way ANOVA. Adult body condition was significantly higher at Gull Island, and there was a significant increase in condition between prelaying and incubation and decrease between incubation and chickrearing (GLM: colony, $F_{1,143}$ = 8.543, P = 0.004; phase, $F_{2,143}$ = 14.642, P < 0.001; Sheffé multiple comparisons, all pairwise effects P < 0.02). However, colony and phase acted independently on body condition (GLM: colony and phase interaction $F_{2,141}$ = 0.615, P = 0.542).

1999

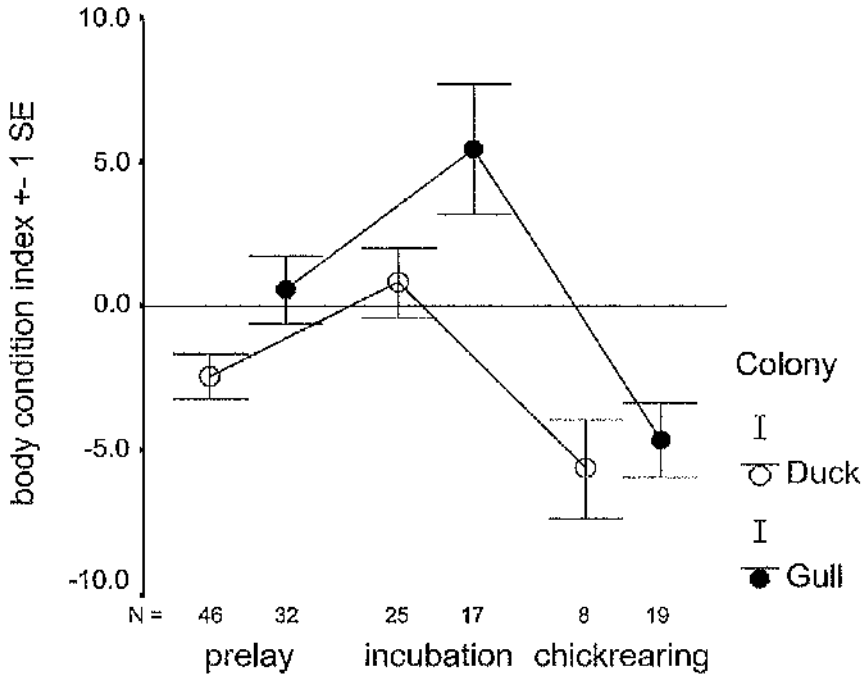
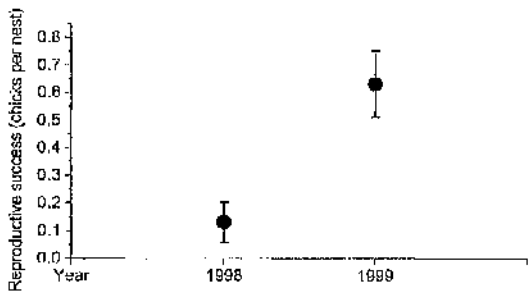
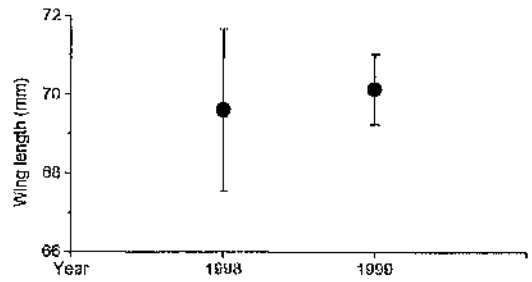
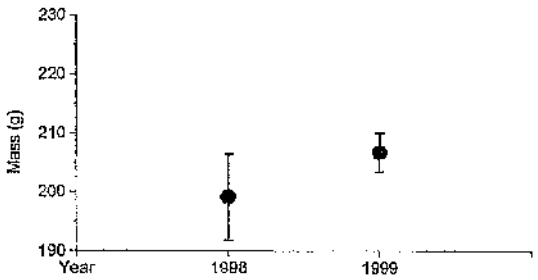

10.0
5.0
0.0
-5.0
-10.0
body condition index +- 1 SE
N = 46 32 25 17 8 19
prelay
incubation
chickrearing
Colony
Duck
Gull

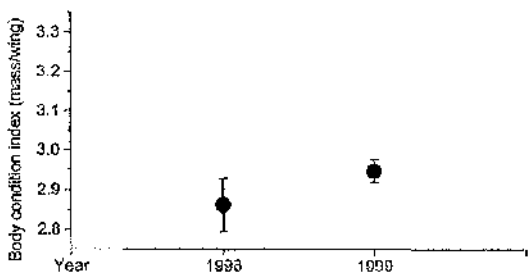
Figure 6. Comparison of mean condition and age parameters ± 1 SE for fledglings at Duck Island in 1998 (left column) and 1999 (right column). Reproductive success differed significantly, and is shown for reference in top panel (see Table 1 for statistics). There were no significant differences between years in fledgling wing length (t_{110} = -0.241, P = 0.810), mass (t_{110} = -0.959, P = 0.340), body condition (t_{110} = -1.226, P = 0.223), or estimated age (t_{110} = -0.241, P = 0.810). The estimated age of captured fledglings did not differ in either year from the age of fledglings determined through observations of productivity plots (open circles in bottom panel; 1998 t_{26} = 0.507, $P > 0.3$; 1999 t_{154} = -1.254, $P > 0.2$).

Duck Island: 1998 & 1999









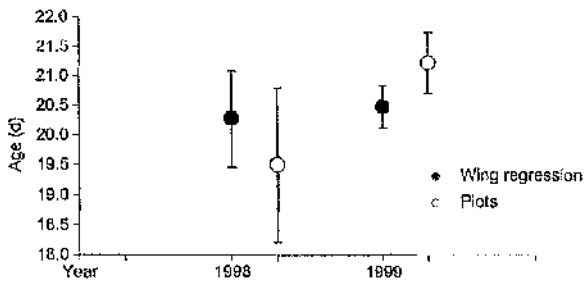


Figure 7. The mass and wing-length relationships for guillemot fledglings at Duck Island in 1998 (closed circles) and 1999 (open circles). The relationships did not differ between years (1998 y = 8.235 + 2.742x, $F_{1,18} = 26.889$, $P < 0.001$; 1999 y = 3.037 + 2.904x, $F_{1,90} = 149.787$; $P < 0.001$; ANCOVA slopes $F_{1,108} = 0.086$, $P = 0.770$; ANCOVA elevations $F_{1,109} = 1.541$, $P = 0.217$).

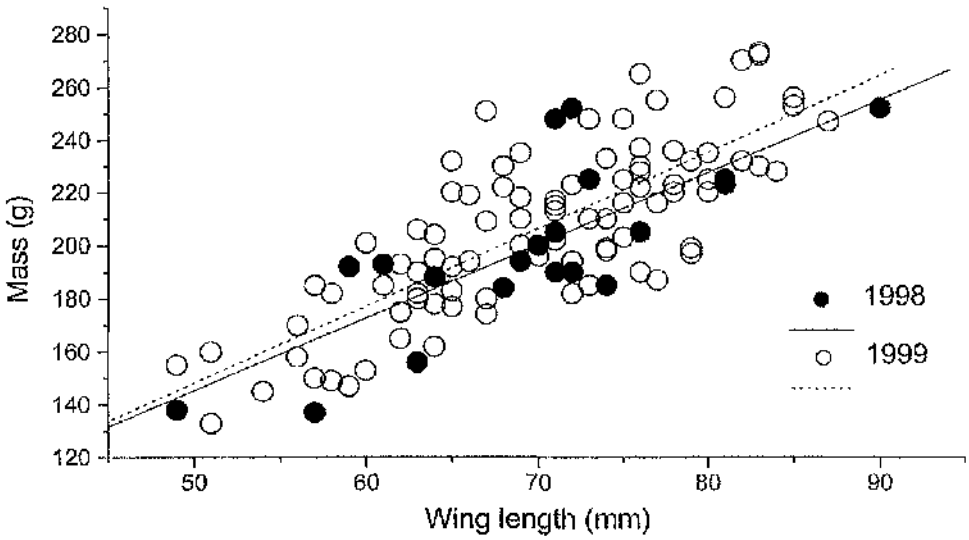
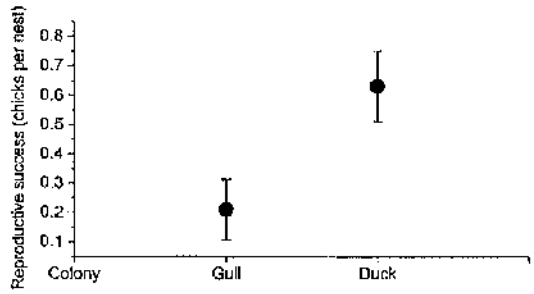
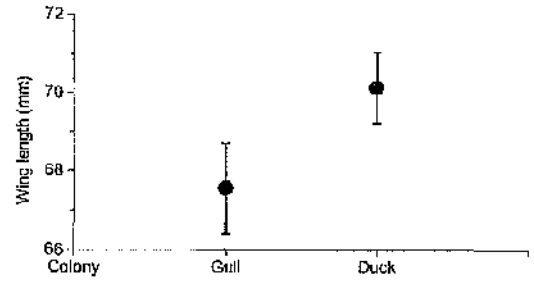
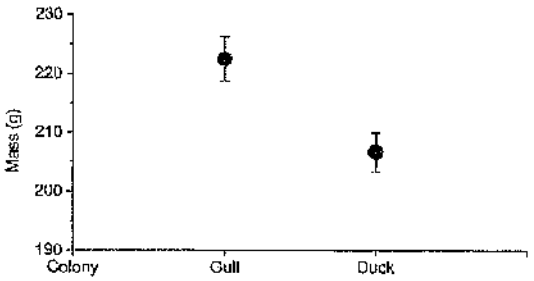

Mass (g)
280
260
240
220
200
180
160
140
120
50
60
70
80
90
Wing length (mm)
1998
1999

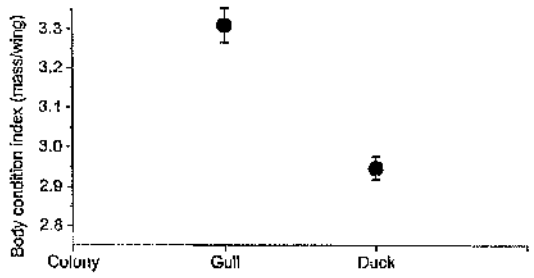
Figure 8. Comparison of mean condition and age parameters ± 1 SE for guillemot fledglings at Gull Island (left column) and Duck Island (right column) in 1999. Reproductive success differed significantly, and is shown for reference in top panel (see Table 1 for statistics). There were no significant differences between colonies in fledgling wing length (*t* test with unequal variances $t_{119} = -1.817$, $P = 0.072$) or estimated age (*t* test with unequal variances $t_{119} = -1.817$, $P = 0.072$), but chicks at Gull Island fledged with greater mass (*t* test with unequal variances $t_{112} = 3.438$, $P = 0.001$) and better body condition ($t_{136} = 6.867$, $P < 0.001$). The estimated age of captured fledglings did not differ at either colony from the age of fledglings determined through observations of productivity plots (open circles in bottom panel; Gull Island $t_{68} = -1.107$, $P > 0.2$; Duck Island $t_{154} = -1.254$, $P > 0.2$).

1999: Gull & Duck Islands









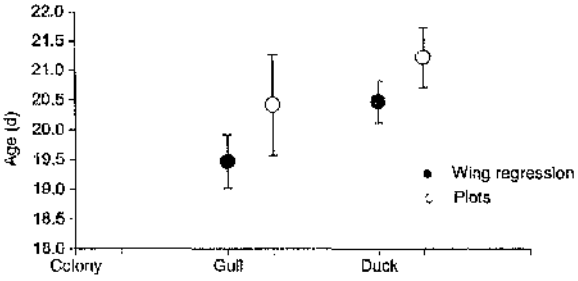
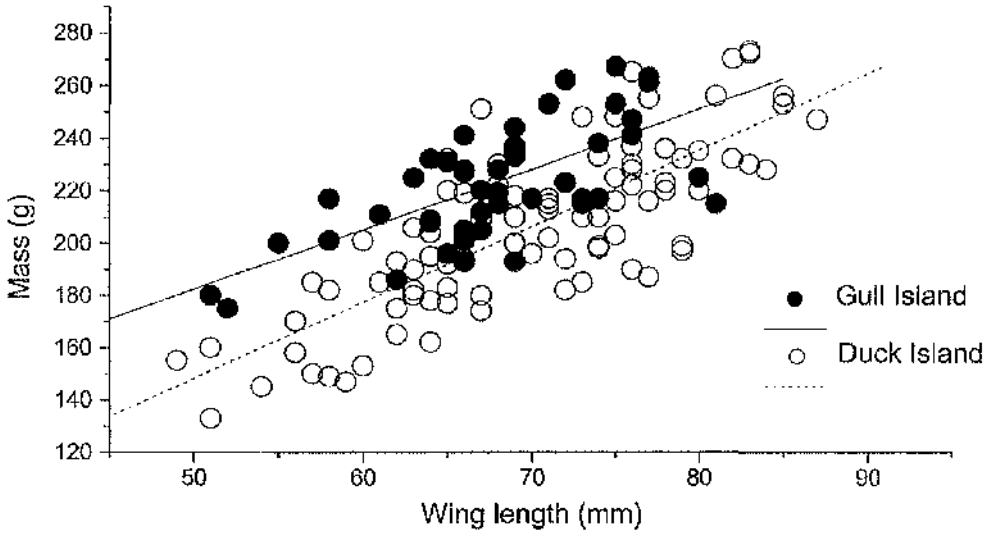


Figure 9. The mass and wing-length relationships for guillemot fledglings at Gull Island (closed circles) and Duck Island (open circles) in 1999 (Gull Island y = 68.164 + 2.285x, $F_{1,45} = 44.167$, $P < 0.001$; Duck Island y = 3.037 + 2.904x, $F_{1,90} = 149.787$; $P < 0.001$). For any structural size, fledglings at Gull Island had greater mass (ANCOVA elevations $F_{1,136} = 43.053$, $P < 0.001$), but the change in mass with wing-length did not differ between colonies (ANCOVA slopes $F_{1,135} = 2.092$, $P = 0.150$).


Mass (g)
280
260
240
220
200
180
160
140
120
50
60
70
80
90
Wing length (mm)
Gull Island
Duck Island

Discussion

This study provides further evidence of the complexity by which avian productivity can be linked to parental and offspring body condition. At a single colony in two years of extremely different productivity (Duck Island in a 'bad' year [1998] and a 'good' year [1999]), we detected no between-year differences in adult body condition; there were consistent changes between phases of breeding, but neither the intensity nor the pattern of those changes correlated to productivity. There was also no linkage apparent in the offspring; chicks in both years fledged at similar age, size, mass, and condition.

In contrast, when we compared two adjacent but oceanographically distinct colonies with highly significant differences in productivity during a single year (1999), we found that productivity had a strong inverse relationship to adult body condition, so that parents at the 'bad' colony (Gull Island) were in better condition than parents at the 'good' colony (Duck Island). Offspring condition was also negatively related to productivity; chicks at the low-productivity colony fledged at a slightly heavier absolute weight, and in much better condition for a given structural size.

The sex of parents did not play a role in either comparison; males and females in this system appear to be balanced in terms of their reproductive effort as measured by body condition changes during breeding, despite egg production costs borne by females during the prelaying period (Monaghan *et al.* 1998).

A key assumption that we make in interpreting these results is that poor productivity translates to poor feeding conditions, and therefore increased parental effort for those parents successfully breeding. Productivity is not normally tightly linked to prey availability in this species, due to the ability of guillemots to buffer

their activity budgets over a range of moderate-to-good feeding conditions (Burger & Piatt 1990; Uttley *et al.* 1994; Piatt & Anderson 1996). But the unusually low productivities observed at Duck Island in 1998 and Gull Island in 1999 indicate that feeding conditions were so poor as to prohibit the majority of parents to successfully complete breeding; we therefore assume that those parents able to fledge chicks were experiencing relatively very demanding conditions. Seen in the context of this assumption, how can our apparently counter-intuitive body condition results be explained?

It is possible that individual quality effects may have overridden the relationships between productivity and condition. We only captured active breeders; perhaps in 'bad' colony-years there was a filtering effect, with only the best quality individuals left breeding late in the season. Long-term studies have shown that individual quality can overcome assumed costs, with high-quality individuals able to both produce greater numbers of offspring and live longer, implying that some individuals could breed more successfully under stressful conditions and not pay the expected penalties in body condition (Aebischer & Coulson 1990). A threshold effect of decreasing body condition driving abandonment of the breeding effort has been suggested (Monaghan *et al.* 1992; Saether *et al.* 1993; Erikstad *et al.* 1997); if this was the case, our study may not have detected it, since birds that abandoned were not captured.

A further possibility is that productivity is an inaccurate between-colony measure of breeding effort and conditions. The assumption that productivity reflects feeding conditions relies on assuming that the groups being compared are composed of individuals with equal mean quality (age and/or breeding experience) and, in colonial birds, are within colonies of similar size, density, and experiencing similar degrees of predation pressure. Equal quality may in fact not be the case in our study;

the two colonies being compared have had very different population trends over the past few decades, with Gull Island (the 'poor' colony in 1999) having a steadily expanding population while the Duck Island (the 'good' colony in 1999) guillemot population has decreased by an order of magnitude over the same time period. One explanation for an expanding population is higher recruitment, which would translate into a greater proportion of young breeders at Gull Island: this could drive productivity measures down, despite feeding conditions that are adequate for more experienced breeders, thereby decoupling productivity and parental effort and distorting between-colony comparisons. However, our comparisons are between colonies with extreme differences in productivity, and we would not expect such a decoupling effect to be fully responsible.

Food supply could vary within seasons, with low food early in the season depressing hatching success but with improving prey availability later in the season allowing the remaining breeders to adequately provision young while maintaining their own condition. We have no information on within-season variation in food supply, but there are two arguments against this explanation for decoupling productivity and adult condition: i) in 'bad' years, both hatching and fledging success were lower, indicating that limits on productivity acted across the season, and ii) breeding phase effects on body condition were consistent across colonies and years, indicating consistent reproductive investment among successful breeders. We note that the difference in fledging success between Gull Island and Duck Island in 1999 was not statistically significant; this could be due to low power resulting from large variances and small sample sizes. However, the difference was of sufficient biological significance to drive overall reproductive success to statistically different levels (Table 2).

A major question arises from our counter-intuitive results: is body condition an adequate proxy for parental reproductive investment? Whether mass loss during breeding is adaptive or results directly from the increased costs of breeding has been the topic of much debate; it is currently held to result from some combination of intrinsic and extrinsic effects. The relative contributions of those effects are likely to remain imprecisely known, but it is generally agreed that differences in mass loss reflect real differences in reproductive costs (Nur 1984; Moreno 1989; Golet & Irons 1999). However, interpreting the absence of mass loss differences is even less straightforward. With the assumption of poor food availability driving poor productivity upheld, it could be that the costs of reproduction do indeed increase as productivity decreases, but without those costs translating into body condition effects. Parents may maintain their body condition despite increasing effort; this should come at some cost to future reproduction, expressed either in reduced future productivity (Gustafsson & Sutherland 1988) or survival (Daan *et al.* 1996). Phenotypic manipulative experiments that directly increased foraging costs in two studies of petrels (Procelliformes) found that reproductive costs were shunted to offspring, resulting in poorer-quality offspring while parental condition was unaltered (Saether *et al.* 1993; Mauck & Grubb 1995). However, another study that increased foraging costs found that both adult and offspring body condition decreased (Weimerskirch *et al.* 1995).

An alternative experimental approach is to increase reproductive demand by increasing the number of offspring; a large number of such studies (mostly in passerines) have shown either negative or neutral effects on parental and offspring condition (reviewed in Stearns 1992). An important limitation of such brood-enlargement studies is that short-lived passerines may already be maximising their per-year reproductive effort as predicted by life-history theory, leaving no buffer

whose reduction could be detected in body condition changes (Golet *et al.* 1998). More relevant to our results, a study on a long-lived seabird (kittiwake *Rissa tridactyla*) showed that parents rearing enlarged broods paid a cost in reduced survival (Jacobsen *et al.* 1995), although that conclusion has been questioned on methodological grounds (Boulinier *et al.* 1997). An experiment using experimentally reduced provisioning effort in rearing the normal brood size of one in the puffin *Fratercula arctica* found no parental body condition differences in the year following manipulation, but did find superior fledging success and offspring body condition in the experimental group (Wernham & Bryant 1998), supporting the hypothesis that a long-lived species will abandon a breeding attempt or reduce offspring quality rather than compromise their own survival. However, workers using multi-year experimental brood reductions in the kittiwake showed a clear cost of normal reproduction among parents raising the modal brood compared to those raising no brood (Golet *et al.* 1998). This cost was mediated through a reduction in body condition followed by reduced overwinter survival (Golet *et al.* 1998; Golet & Irons 1999).

Taken together, these studies indicate that reproduction is costly, and that increased reproductive effort should result in either: i) abandonment of breeding, ii) reduced investment in breeding (hence reduced offspring quality), iii) or increased investment that could be expressed either in reduced parental condition, survival, or both (Drent & Daan 1980; Stearns 1992). In the present study, the level of abandonment was unknown, since it was not possible to determine whether egg and chick loss was due directly to abandonment or to another factor (e.g. predation).

Our results gave no indication of increases in reproductive effort being shunted to offspring. In the two contrasting productivity years at Duck Island, successfully fledging offspring were equal in all measured parameters. At the two

colonies with contrasting productivity, fledglings from the 'poor' colony were actually in better condition at fledging. The condition of young at independence has been positively correlated with subsequent survival in a variety of avian (Perrins 1965; Parsons 1970; Perrins *et al.* 1973; Jarvis 1974; Ankney 1980; Galbraith 1988) and mammalian species (Thorne *et al.* 1976; Guinness *et al.* 1978). In seabirds, positive relationships have been found between food supply, chick growth, and chick survival (Hamer *et al.* 1991). Between two years of sharply different food availability and reproductive success, Uttley *et al.* (1994) found common guillemot chick growth rate to be equal, but chicks of a given size were heavier in the year of higher productivity. Guillemot chicks fledge at highly variable masses, and it has been suggested that colony-specific effects dominate the variation (Gaston *et al.* 1983), likely due to some interaction between colony size and foraging range. Interestingly, two large-scale studies in guillemots have shown little relationship between chick fledging age and condition and subsequent survival and recruitment (Hedgren 1981; Harris *et al.* 1992). This could be in part due to the 'intermediate' development strategy in guillemots whereby fledglings continue to receive parental care for up to two months post-fledging. (Gaston 1985). Still, it is reasonable to assume that chicks leaving the colony in better condition must gain some future advantage.

As expected, our study provides mixed evidence for a relationship between reproductive demand (food availability during the breeding season) and investment (using body condition as an index). We have shown that a variety of plausible explanations and scenarios could be applied to our results. That no correlation exists between demand and investment at one colony, while an inverse relationship exists between two colonies, serves in part to emphasise the importance of colony-specific factors in considering reproductive trade-offs in seabirds (Gaston 1985). Our results further highlight that resource allocation, investment, and trade-offs in long-lived

species must be seen as part of an integrated strategy across lifetimes, so that results appearing counter-intuitive in the short-term may in fact maximise fitness in the long term. Knowing more of the variables involved in the correlations discussed here (e.g. direct measurement of parental effort; adult survival; offspring survival) would strengthen our interpretations. But a more complete understanding of these trade-offs could best be achieved using experimental manipulations, ideally across multiple breeding seasons.

Chapter Five

If at first you don't succeed? Effects of egg loss on reproductive performance in common guillemots *Uria aalge*

Introduction

That reproduction is costly is a central tenet of life history theory (Stearns 1992). What this means for iteroparous breeders is that there is a need to balance the level of investment in the current reproductive event with the consequences for future performance. However, the level of investment required for successful breeding in a particular year may vary in relation to intrinsic and extrinsic circumstances. The individual's own state or that of its mate may alter between years (McNamara & Houston 1996), as may environmental factors such as weather, food availability or predation levels (Benton & Grant 1996; Tolonen & Korpimaki 1996; Schekkerman *et al.* 1998). Individuals therefore need to respond to such changing circumstances by making appropriate reproductive decisions.

In seasonal environments, deciding when to begin is an important component of the breeding event (Brinkhof *et al.* 1993; Lepage *et al.* 1999). This has been particularly well studied in birds, with the general finding that the timing of egg laying is tailored relatively closely to seasonal changes in food availability (Perrins 1970; Daan *et al.* 1988; Verhulst & Tinbergen 1991; Nager & VanNoordwijk 1995). Nonetheless, intra-specific differences in the timing of avian breeding within a season can be considerable. These are generally linked to differences in individual state (McNamara & Houston 1996), with older, more experienced or higher quality individuals breeding earlier and having the highest reproductive success. Early-laying pairs often produce larger clutches, rear a greater number of fledglings, and more of their fledglings are recruited into the breeding population (e.g. Hedgren & Linnman 1979; Drent & Daan 1980; Harmon *et al.* 1988; Hochachka 1990; Brouwer *et al.* 1995). While this difference in performance may arise from seasonal changes in the

environment experienced (Verhulst & Tinbergen 1991), some studies have demonstrated that when the timing of reproduction in early laying birds is experimentally altered (for example by removal of the first clutch or by extending incubation) such individuals still perform better than unmanipulated conspecifics breeding at the same time; this is despite the experimental protocol resulting in their having incurred higher costs prior to the clutch hatching (Daunt *et al.* 1999; Hipfner *et al.* 1999). However, this does not mean that increased investment in egg production and incubation has no fitness consequences for individuals (Monaghan & Nager 1997). The time scale and effects of investment increases may vary with individual quality (Heaney & Monaghan 1996), and their magnitude is also likely to vary with environmental circumstances (Haftorn & Reinertsen 1985).

Clutch loss due to predation is a persistent feature of many avian reproductive environments. Replacement laying potentially doubles egg production costs and, depending on when loss occurs, incubation costs may also increase. Clutch loss also substantially delays breeding, forcing relaying birds to breed in an environment that may differ from the one originally selected. This has an added dimension in colonial birds because of the importance of synchronous reproduction, which is considered to give both foraging and anti-predator benefits (Danchin & Wagner 1997; Beauchamp 1999). The decision as to whether or not to replace the lost egg, and how much to invest in that egg, is therefore likely to be state-dependent and will vary in relation to an individual's physiological state, environmental conditions, and the intensity of synchronous breeding.

Colonial common guillemots *Uria aalge*, and the closely related Brünnich's guillemots *Uria lomvia*, generally show marked seasonal declines in reproductive output, positive correlations between success and both density and local synchrony,

and seasonal declines in the probability of replacement layings (Birkhead 1977; Gaston & Nettleship 1981; Birkhead & Nettleship 1987; Wanless & Harris 1988; Boekelheide *et al.* 1990; Hatchwell 1991). Most correlative studies on these species have found that replacement eggs following natural loss have a low mean success (Hedgren 1980; Birkhead & Nettleship 1987; Harris & Wanless 1988; Boekelheide *et al.* 1990; Hatchwell 1991). Recent work using experimental egg removals from early-laying pairs has found success of the replacement eggs to equal that of first eggs, and to exceed that of first eggs laid concurrently (Hipfner 1997). This indicates that the probability and success of replacement laying may be determined not by time in the season or environmental conditions, but by some combination of parental quality (Hipfner 1997) and local synchrony (Hatchwell 1991). The observed seasonal decline in replacement layings can therefore be ascribed to the fact that lower quality, often late laying, birds are more likely to lose their eggs under natural circumstances (Hipfner *et al.* 1999). However, at least one observational study found no difference in success between first and relaid eggs (Murphy & Schauer 1994). It seems likely that the extent to which even high-quality individuals can compensate for the added costs of replacement laying varies with environmental conditions. To investigate this hypothesis, we examined the response of individuals of different quality to induced egg loss in a declining, small colony of common guillemots where environmental conditions were known to be relatively poor. We measured the probability of relaying, the quality of replacement eggs, and chick growth and survival in comparison with conspecifics initially breeding at the same time but which did not lose their first egg. We predicted that responses to egg loss would be state-dependent and relatively severe at this colony in comparison with what has been found in studies conducted under good environmental conditions.

Methods

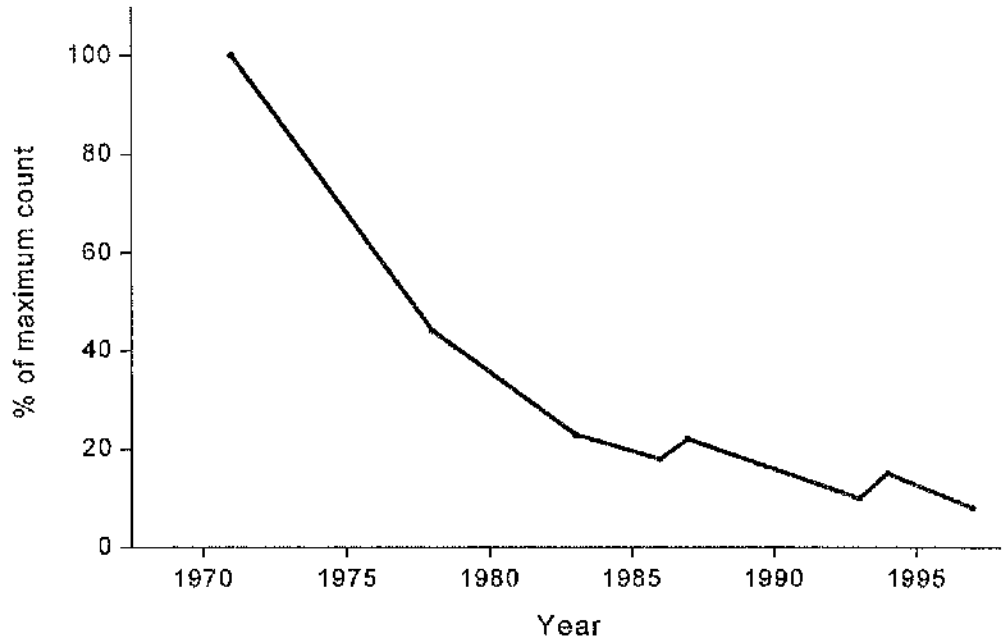
Study location and background

Our work was conducted at the common guillemot colony on Duck Island, Cook Inlet, Alaska (60° 09′ N, 152° 34′ W) between June-September 1999. Duck Island currently supports ca. 2500 guillemots, representing a steady decline to ca. 10-20% of maximum counts made in the early 1970s (Fig. 1). A number of independent measures made concurrently with this study (nearshore forage fish abundance; offshore midwater fish availability; adult foraging trip duration and 'loafing' time at the nest; stress hormone levels) provide strong evidence that guillemots breeding at Duck Island experienced food shortages during the 1995-1999 breeding seasons and are relatively highly stressed (Kitaysky *et al.* 1999; Robards *et al.* 1999; Zador & Piatt 1999; A. Kitaysky *et al.* unpublished data; J.F. Piatt *et al.*, unpublished data).

Egg loss through predation is not uncommon at this colony. The island supports a colony of ca. 500 glaucous-winged gulls (*Larus glaucescens*) and is regularly visited by ravens (*Corvus corax*), bald eagles (*Haeliatus leucocephalus*), and peregrine falcons (*Falco peregrinus*). Gulls and ravens in particular were regularly observed predating guillemot eggs; eagles and falcons took eggs directly to a lesser extent, but also facilitated gull and raven egg predation by flushing adults off their nesting areas.

Approximately half of the guillemots on Duck Island breed on inland areas consisting of bare soil at cliff tops, defoliated at ground level, with a variable secondary covering of woody bushes. All the nest sites used were in this habitat, since it greatly facilitated observation and manipulation. We monitored the breeding chronology and breeding success of a study plot of common guillemots following a modified version of the Type I observational methods detailed by Birkhead &

Figure 1. Changes in the numbers of common guillemots breeding at Duck Island, Alaska. Data are shown as percentages of the maximum count made in 1971.


% of maximum count
100
80
60
40
20
0
1970
1975
1980
1985
1990
1995
Year

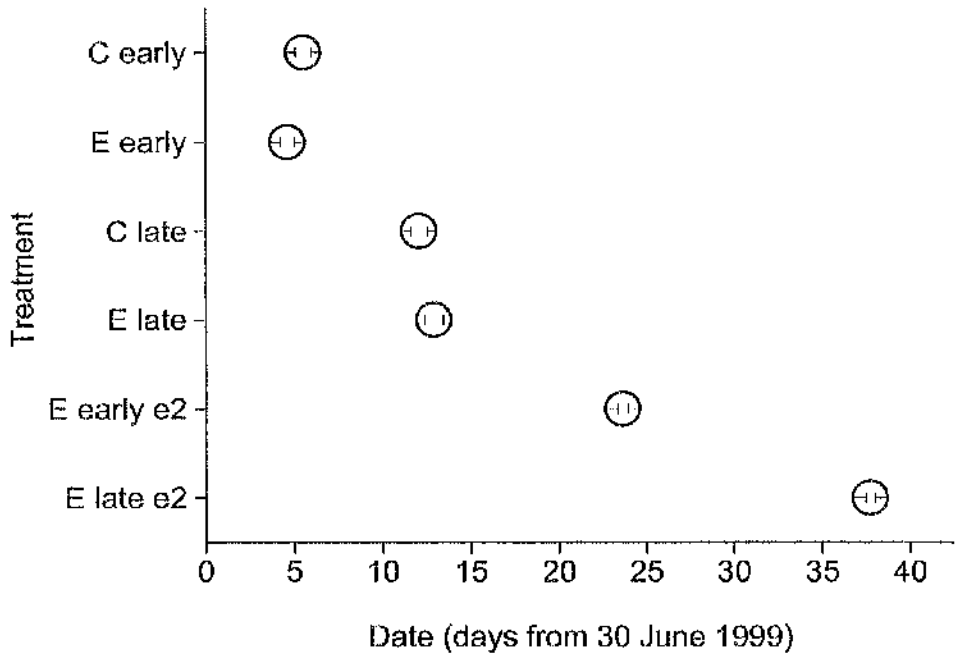
Nettleship (1980), using a hide located 1-10 m distant from nest sites. To ensure that nest sites were occupied by the same pair over the season, most pairs involved in this study included at least one adult that was uniquely colour-ringed; sites without colour-ringed adults were clearly defined by natural landmarks, allowing reasonable certainty that relaying pairs were the same as the original nesters. Replacement egg colour and pattern were also compared to photographs of first eggs to further confirm consistency in nest-site occupancy (Birkhead & Nettleship 1982). Guillemots in the study plot laid their first eggs over a 20 day period, from 1 July to 19 July, with a median laying date of 10 July.

Experimental design

To test our predictions of the costs of egg loss, we assigned birds to one of four treatment groups: early-laying and late-laying controls, rearing their first eggs, and early and late experimentals, rearing a replacement egg. Because the majority of eggs laid prior to the median laying date have been shown in guillemots to come from older, higher-quality pairs (Hipfner 1997), we used median laying date to delineate early and late breeding treatments. Control Early (C early) and Experimental Early (E early) pairs were randomly chosen from among those pairs that had laid a first egg prior to the median laying date, and Control Late (C late) and Experimental Late (E late) pairs were randomly chosen from among those pairs laying first eggs on or after the median laying date. The pattern of laying dates of birds in the control and experimental treatments are shown in Fig. 2.

To create the two experimental treatment groups, we removed first eggs from the E early and E late pairs during several short collection visits (under Alaska State and U.S. Federal permits). Control parents were flushed off their egg in the same manner, but the egg was not removed. In order to obtain data on the quality of

Figure 2. The timing of laying of first eggs in the control early and late groups (C early & C late), and experimental early and late groups (E early & E late) whose first eggs were removed, with 1 SE bars shown within circles. Also shown are the mean dates of laying of the subsequent replacement eggs (E early e2 & E late e2). There was no difference in first-egg laying dates of the C early (mean = 5.53 ± 0.46, n = 17) and E early groups (mean = 4.62 ± 0.38, n = 26; t_{41} = 1.510, P = 0.14) or between the C late (mean = 12.07 ± 0.47, n = 15) and E late groups (mean = 12.91 ± 0.53, n = 11; t_{24} = -1.178, P = 0.25). After pooling the treatments into early and late groups, mean first-egg laying dates differed by 7.4 d (early mean = 4.98 ± 0.30, n = 43; late mean = 12.42 ± 0.35, n = 26; t_{67} = -15.664, P < 0.001). Replacement eggs of the E early group were laid significantly later than first eggs of the C late group (E early replacement mean = 23.64 ± 0.30; n = 25; t_{38} = -21.566, P < 0.001) and significantly earlier than E late replacements (E late replacement mean = 37.75 ± 0.25; t_{27} = -18.111, P < 0.001).


C early
E early
C late
E late
E early e2
E late e2
Treatment
0
5
10
15
20
25
30
35
40
Date (days from 30 June 1999)

replacement eggs, we removed the second laid eggs from a subset of E early pairs during a single visit. We did not remove any E late replacement eggs, since the number relaying in this group was very small. We removed all eggs using a 'Helping Hand' clawed tool (a grasping extension for disabled people), modified with padded jaws and attached to a telescoping 8 m fibreglass pole. The claw's trigger was fitted with a trailing line, allowing operation from a hide. The majority of attending parents remained in contact with their nest site during egg-removal, and parental behaviour in the targeted area appeared normal within *ca.* 1 hour. Gulls were kept away from eggs left unprotected in removal activities by judicious use of small pebbles or sticks.

Nest sites were checked daily between 1000-1800 ADT for the presence of eggs or chicks. Fledging age is taken as the inclusive number of days from the hatching date to the day prior to the date when the chick was first recorded as not present. Hatching success is taken as the proportion of eggs hatching, fledging success the proportion of hatched chicks that fledged, and breeding success the proportion of nest sites where an egg was laid from which a chick fledged (Birkhead & Nettleship 1980). Since 15 days is the minimum nest departure age in common guillemots (Gaston & Jones 1998), chicks were considered to have 'fledged' successfully if they disappeared from the nest site >=15 d after hatching; any chicks that disappeared prior to this were assumed to have died. To investigate the validity of this assumption, we compared the wing length distribution of a random sample of non-experimental chicks captured while making their way to the sea to the estimated wing length (using a wing length-age regression on experimental chicks) of experimental chicks at 14 d.

Chick growth

Due to the excessive colony disturbance involved in chick captures, we were not able to repeatedly capture individual chicks. We therefore use two alternative approaches to compare chick growth; structural size in relation to age, and mean body condition.

Chicks from C early, C late, and E early treatments (there were no E late chicks) were captured using a fibreglass pole and wire hook once during the linear growth phase (4-14 days). Chick capturing bouts were timed to minimise disturbance whilst ensuring the necessary variation in growth stage for calculation of growth rates; weight (g), head-plus-bill, tarsus, and wing lengths (to longest primary covert) were measured in millimetres. After processing, chicks were returned to the vicinity of their nest site using the same tool. Most chicks were reunited with their parent after <10 min.

To obtain an index of body size for chicks, we performed a principal components analysis (PCA) on the linear measurements (Freeman & Jackson 1990). The resulting coefficients had consistent loadings (head-plus-bill 0.58, tarsus 0.58, wing 0.57), and the first principal component accounted for 95% of the variance in the original measures. Measurement data were multiplied by the coefficients, and added together to produce a PCA factor score for each chick, hereafter called the 'body size index'. We regressed body size indices on the age (days) of known-age chicks to measure structural growth rate within and between groups. Regression slopes (representing growth rate) and elevations were compared using ANCOVA. We then regressed body mass (grams) of all control chicks on the body size index to generate an equation predicting the mass of a chick, given a known size (mass = 190.20 + [19.48*body size index], n = 13, r^2 = 0.65, P = 0.001). We used residuals from this regression expressed as a percentage of the predicted mass to calculate a condition index for all chicks (Golet & Irons 1999; Jakob *et al.* 1996).

Parental condition

In order to establish whether variation in early-season parental body condition may be related to variation in the response to egg loss, we captured a random sample of adults in all four experimental groups during egg removal visits. Captures were made 1-9 days after egg laying. We used a telescoping fibreglass pole fitted with a noose for captures, then measured body mass and head-plus-bill, wing, and tarsus length. Adults were released ca. five minutes after capture, and usually returned to their nest site within ten minutes of capture. Body size and condition were assessed using the same methods as described above for chicks. PCA component loadings were 0.544 for head-plus-bill, 0.607 for wing, and 0.579 for tarsus, accounting for 54% of variance in the original measures. The adult body size-mass regression equation was predicted mass = 1028.86 + 29.358 * (body size index); $n = 46$, $r^2 = 0.33$, $P < 0.001$.

Egg quality

We measured the length and maximum breadth of each removed egg (± 0.1 mm) using vernier callipers. Egg volume indices were calculated using the formula (length * breadth^2) of Birkhead and Nettleship (1984). Fresh eggs were boiled for ca. 12 min within 48 h of collection, placed inside a plastic bag, and stored in a freezer until later analysis of composition. In the laboratory, we weighed each egg, then thawed and separated the eggs into shell, yolk, and albumen. Each component was dried separately at 60°C to constant mass. Components were reweighed to determine dry mass and percent water content. Since nearly all egg lipid is contained in the yolk (Carey 1996), we measured the lipid content of the yolk only. We extracted lipid from the yolk using Soxhlet extraction with petroleum ether as a solvent (Dobush *et al.* 1985). Samples were then dried again and reweighed, and lipid content determined

by subtraction. The boiling and freezing processes altered egg water content, and we therefore present comparisons in dry mass terms only.

Statistical analyses were carried out using SPSS; all tests are two-tailed and considered significant at probability levels less than α=0.05. Means are given ± 1 SE.

Results

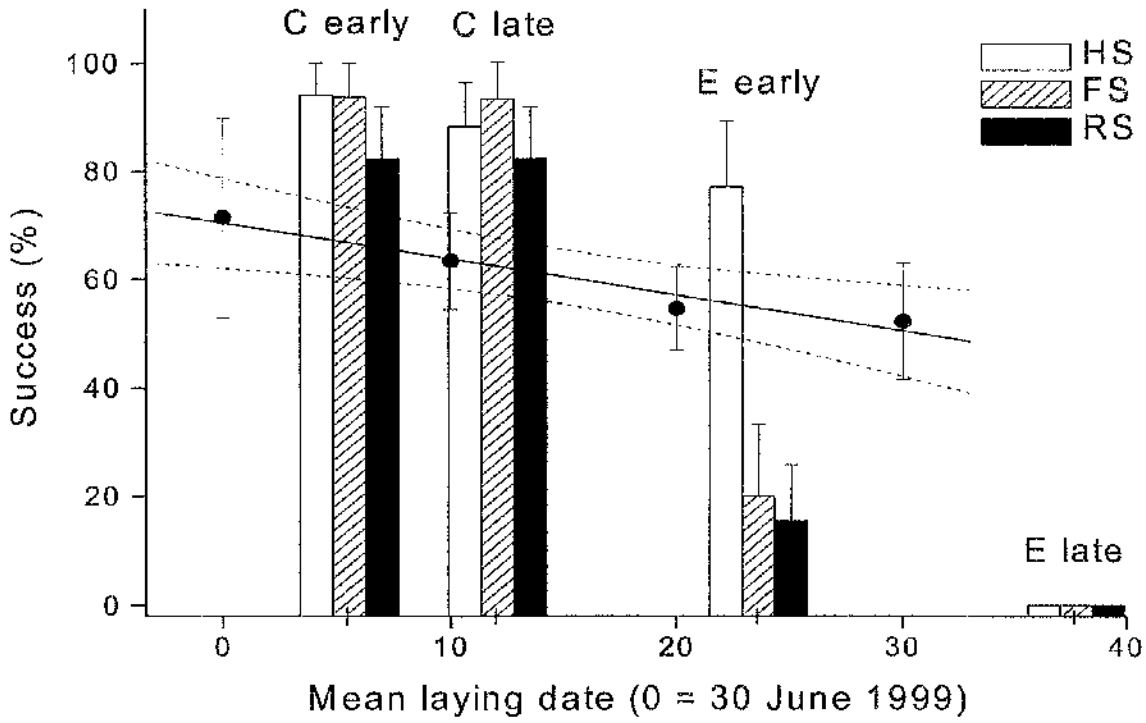
Reproductive success of Experimental and Control groups

There was little seasonal decline in breeding performance between the control groups, and the hatching, fledging, and reproductive success of C early pairs was similar to that of C late pairs (Fig. 3). E early pairs rearing a replacement egg had similar hatching success to the early and late laying control pairs; however, their fledging and reproductive success was much lower than C early and C late pairs. The few E late pairs that relaid had zero hatching, fledging, or reproductive success (Fig. 3). Using productivity data from elsewhere in the colony, we plotted the general seasonal pattern of productivity, which declined from ca. 70% to ca. 55% over a thirty-day period of egg-laying (Fig. 3). Comparing this with the decline in performance of the replacement-laying birds demonstrates that the reproductive success of replacement eggs in the E early group was much lower than that of concurrently-laid first eggs (Fig. 3).

Probability and timing of egg replacement

There was a significant difference between the early and late experimental groups in the proportion of pairs that laid a replacement egg, with 96% of E early pairs laying a replacement egg compared to only 36% of E late pairs (E early: 25/26 pairs; E late:

Figure 3. Reproductive performance of the control early (C early; n = 17) and late (C late; n = 17) and experimental early (E early; n = 13) and late (E late; n = 4) treatment groups, expressed as percentage proportions ± 1 SE. There were no differences between control treatments in hatching success (HS; Fisher's exact test, P = 0.20), fledging success (FS; Fisher's exact test, P = 0.74) or reproductive success (RS; Fisher's exact test, P = 0.55). The hatching success of experimental early replacement eggs was similar to controls (Fisher's exact tests: C early v E early P = 0.20; C late v E early P = 0.09). However, the fledging and reproductive success of experimental pairs rearing chicks from replacement eggs was significantly lower than control pairs (Fisher's exact tests: C early v E early; FS $P < 0.001$; RS $P < 0.001$; C late v E early; FS $P < 0.001$, RS $P < 0.001$). The regression line represents the general seasonal decline in reproductive success, plotted from results of nests elsewhere in the colony, grouped into 10 day periods and shown with 95% confidence bands (y = 70.53 - 0.666x) total n = 104; r^2 =0.95; $F_{1,3}$ = 41.328; P = 0.023).


C early
C late
E early
E late
HS
FS
RS
Success (%)
100
80
60
40
20
0
0
10
20
30
40
Mean laying date (0 = 30 June 1999)

4/11 pairs; Fisher's exact test, $P < 0.001$). Time taken to produce the replacement egg was shorter in the E early group, ranging from 13 to 18 days (mean = 15.24 ± 0.25 d, n = 25) compared to 17 to 18 days in the albeit small number that relaid in the E late group (mean = 17.75 ± 0.25 d, n = 4; Mann-Whitney U test = 4.00, P = 0.003).

Within the early laying experimental treatment, time for which eggs had been incubated prior to egg removal ranged from one to seven days (mean = 3.81± 0.36; n = 26). Since nearly all birds in this group relaid, incubation duration did not appear to influence the probability of relaying, nor did it influence the time taken to produce the replacement egg (r^2 = 0.07, ns). Relaying interval was, however, significantly influenced by laying date of the first egg, with later-laying individuals in the E early group producing the second egg faster (Fig. 4).

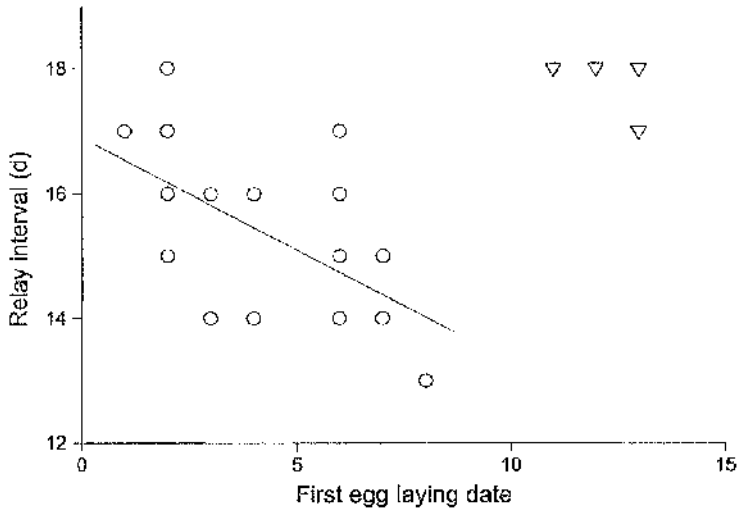
Eggs in the E late group had been incubated for slightly longer before collection (4-9 days, mean = 6.82 ± 0.55 d; n = 11; difference from E early group significant, $F_{1,35}$ = 20.84, P<0.001), but again incubation duration did not appear to influence probability of relaying in the E late group (E late relaying: incubation duration mean = 7.75 ± 0.48 d, n = 4; E late not relaying: incubation duration mean = 6.29 ± 0.78 d, n = 7; Mann-Whitney U test = 8.50, P = 0.291). The small number (4) of late pairs that laid a second egg precluded detailed analyses of factors influencing their relaying intervals, but there was an indication of much longer relaying intervals in the E late group than would be predicted by the decreasing interval with increasing laying date seen in the E early group (Fig. 4).

Parental Condition

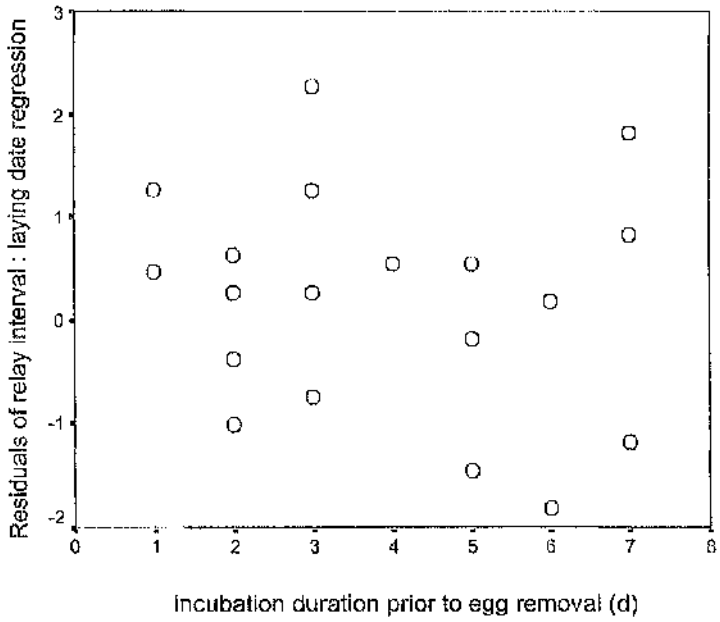
Birds in the treatment groups began the breeding season in similar condition; we found no differences between groups in mean body condition indices (Kruskal-Wallis test; H = 0.803; df = 3; P = 0.849).

Figure 4. The relationship between first egg laying date, relaying interval, and incubation duration prior to egg removal. (a). Relationship between the first-egg laying dates and relaying intervals for birds in the E early group (open circles; y = 16.898 - 0.360x; $r^2 = 0.32$, $F_{1,23} = 10.99$, $P = 0.003$). For comparison, the laying dates of the four experimental late treatment birds that produced a second egg are shown by open triangles (sample sizes too small for analysis). (b). Residuals of E early regression against incubation duration prior to removal, demonstrating that incubation duration explains no additional variance in the relaying intervals. A stepwise multiple regression using E early group laying date and incubation duration as independent variables and relaying interval as the dependent variable excluded incubation duration from the model ($t_{23} = -1.013$, ns), leaving laying date as the significant predictor ($t_{23} = -3.316$; $P = 0.003$).

(a)


Relay interval (d)
18
16
14
12
0
5
10
15
First egg laying date

(b)


Residuals of relay interval : laying date regression
3
2
1
0
-1
-2
0
1
2
3
4
5
6
7
8
Incubation duration prior to egg removal (d)

Egg Quality

First eggs from early pairs were larger and heavier than first eggs from late pairs (Table 1). Among early-laying pairs, first eggs and replacement eggs laid by the same female were strongly correlated in both volume (r_{10} = 0.882, P = 0.001) and dry mass (r_{10} = 0.738, P = 0.015), indicating that birds that laid a relatively large first egg also laid a large replacement egg. However, replacement eggs were smaller. Replacement eggs averaged 2.54 ± 2.45% smaller in volume than first eggs laid by the same female (paired t_9 = 3.18, P = 0.011). Measured in dry mass terms, replacement eggs averaged 7.78 ± 4.04 % smaller than first eggs laid by the same female (paired t_9 = 5.58, P < 0.001), and tended to be larger than concurrently-laid first eggs, though this effect was not significant (Fig. 5). The percentage difference in volume index between first and replacement eggs was unrelated to laying date of the first egg (r^2 = 0.01, $F_{1,8}$ = 0.041, P = 0.844), incubation duration prior to removal of the first egg (r^2 = 0.01, $F_{1,8}$ = 0.041, P = 0.844), or relaying interval (r^2 = 0.143, $F_{1,8}$ = 1.335, P = 0.281). The percentage difference in dry mass between first and replacement eggs was also unrelated to laying date of the first egg (r^2 = 0.22, $F_{1,8}$ = 2.244, P = 0.172), incubation duration prior to removal (r^2 = 0.22, $F_{1,8}$ = 2.244, P = 0.172), or relaying interval (r^2 = 0.00, $F_{1,8}$ = 0.034, P = 0.858).

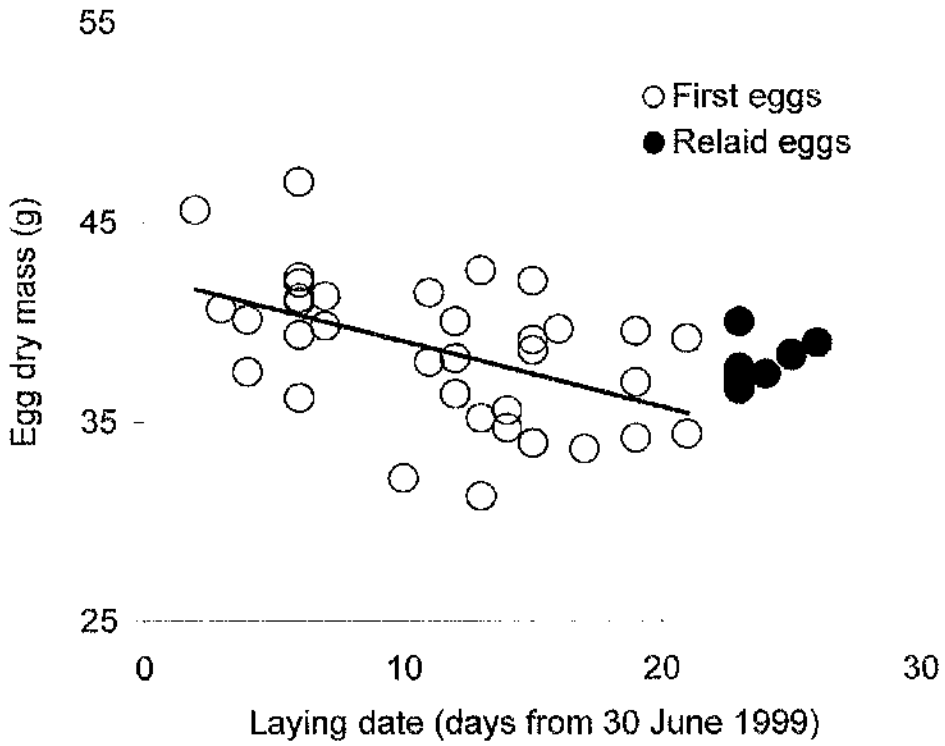
We examined the composition (shell, albumen, lean yolk, and lipid) of E early first and replacement eggs and C late first eggs in terms of both absolute (dry mass g) and relative (% of total) differences. Results are shown in Table 1. Comparing the first eggs of E early and C late birds revealed significant absolute differences, with C late first eggs comprising less lean yolk and lipid mass. However, shell and albumen dry mass did not differ. There were no relative differences in composition. Paired comparisons of E early first and replacement eggs showed similar absolute differences as between E early and C late first eggs, and also no relative differences.

The constituents of C late first eggs and E early replacement eggs differed neither in absolute nor in relative terms.

Table 1. Mean size and composition of eggs from the treatment groups. Comparisons between paired first (e1) and replacement (e2) eggs from the experimental early (E early) group involved paired *t*-tests for mass values; percentage values were compared using non-parametric Wilcoxon's matched pair tests. Also shown is the result of an unpaired comparison of first eggs from the control late (C late) group and first and replacement eggs from the E early group, using one-way ANOVA with Bonferroni multiple comparisons; percentage values were arcsin transformed for analysis. Asterisks denote significant differences at the $P < 0.05$ (*), < 0.01 (**), and < 0.001 (***) levels.

	E early first egg	Paired *P*	E early replacement	C late first egg	*P* E early e1	*P* E early e2
n =	10		10	22		
Volume index (cm^3)	223.00 ± 3.75	*	217.30 ± 3.67	209.20 ± 4.32	ns	ns
Dry mass (g)	41.10 ± 0.79	***	37.82 ± 0.33	37.10 ± 0.68	**	ns
Shell dry mass (g)	14.59 ± 0.33	**	13.45 ± 0.26	13.50 ± 0.30	ns	ns
Albumen dry mass (g)	7.34 ± 0.32	s	6.96 ± 0.23	6.86 ± 0.23	ns	ns
Lean yolk mass (g)	7.58 ± 0.24	**	6.83 ± 0.15	6.43 ± 0.16	**	ns
Yolk lipid mass (g)	11.59 ± 0.28	**	10.58 ± 0.24	10.31 ± 0.24	*	ns
Shell as % of egg	35.48 ± 0.34	ns	35.55 ± 0.57	36.37 ± 0.41	ns	ns
Albumen as % of egg	17.88 ± 0.73	ns	18.42 ± 0.63	18.49 ± 0.49	ns	ns
Lean yolk as % of egg	18.44 ± 0.42	ns	18.06 ± 0.35	17.33 ± 0.27	ns	ns
Yolk lipid as % of egg	28.27 ± 0.52	ns	27.97 ± 0.60	27.81 ± 0.50	ns	ns

Figure 5. Change in egg dry mass with season. First egg mass declines significantly with laying date ($n = 35$; $r^2 = 0.242$; $F = 10.553$; $P = 0.003$). Replacement eggs were laid later than first eggs (mean laying date = 23.7 ± 0.3 d) but their masses were larger than predicted by the seasonal decline (above the regression line), though due at least in part to lack of concurrent data this trend was not significant (testing difference between means, using SE of predicted value at 23.7 d, $t_{44} = 1.47$; $P = 0.14$).


55
45
35
25
Egg dry mass (g)
First eggs
Relaid eggs
0
10
20
30
Laying date (days from 30 June 1999)

Chick growth

The duration of the incubation time to successful hatching did not differ between early and late birds, or between birds rearing first and replacement eggs, (C early mean = 33.69 ± 1.08 d, n = 16; E early replacement egg mean = 33.00 ± 1.15 d, n = 10; C late mean = 33.27 ± 1.58 d, n = 1.58; ANOVA $F_{2,28} = 0.367$, $P = 0.696$)

Structural growth rate of chicks during the linear phase did not differ among treatments (Fig. 6), but the elevations of the growth rate regressions for the C late chicks and replacement-egg chicks of the E early groups were significantly lower than the C early group, indicating smaller size at hatching, as expected from the difference in egg size. Comparing condition indices (see Methods) among groups using one-way ANOVA tests revealed no significant differences, although there was some indication that chicks from the E early group were in poorer condition compared to the C early and C late groups (Fig. 7).

Chicks from first eggs of early and late pairs fledged at similar mean ages (C early mean = 20.13 ± 3.12 days, n = 16; C late mean = 18.53 ± 3.34 days, n = 15; t_{29} = 1.374; $P = 0.180$). All experimental replacement chicks except one disappeared prior to reaching 15 d; we assume that these chicks died immediately or after premature fledging. Experimental chicks tended to die when they were relatively large; the mean age at which E early chicks disappeared was 12.7 ± 2 d (n=10; significantly younger than chicks from first eggs; one-way ANOVA and Bonferroni multiple comparison test with C early, C late, E early; $F = 19.950$, $P < 0.001$). To check on the assumption that these chicks had died, we regressed wing lengths against known ages, with the resulting linear growth equation ($y = 23.056 + 1.969x$; n = 6; $F = 9.286$; P = 0.038) predicting a wing length of 51 mm for a 14-day old experimental chick. A separate data set (from the same colony; see Chapter Three) comprising 235 random

captures of unmanipulated chicks on their way to the sea during 1997-1999 showed that <1% (2/235) of chicks fledge with a wing length <= 51 mm.

Figure 6. Structural growth rate of chicks from Control Early (C early), Control Late (C late), and Experimental Early (E early) treatment groups. We used least-squares regression with age as the independent variable and size (PCA score) as the dependent (C early $y = -2.681 + 0.347x$; $r^2 = 0.90$, $F_{1,6} = 66.59$, $P < 0.001$; C late $y = -4.617 + 0.398x$; $r^2 = 0.96$, $F_{1,2} = 71.084$, $P = 0.014$; E early $y = -3.721 + 0.331x$; $r^2 = 0.86$; $F_{1,4} = 31.365$, $P = 0.005$) to estimate growth during the linear phase. There was no difference in slope between the treatments (ANCOVA, treatment effect on size with age (d) as the covariate, treatment as the factor, and age:treatment as the interaction term: Interaction $F_{2,12} = 1.191$, $P = 0.337$). Elevations of the C late and E early groups also did not differ (Treatment, with NS interaction dropped from the model, $F_{1,7} = 2.234$, $P = 0.179$), but the elevation of the C early group was significantly higher than both the C late group (Treatment, with NS interaction dropped from the model, $F_{1,9} = 10.708$, $P = 0.010$) and the E early group (Treatment, with NS interaction dropped from the model, $F_{1,11} = 10.016$, $P = 0.009$).

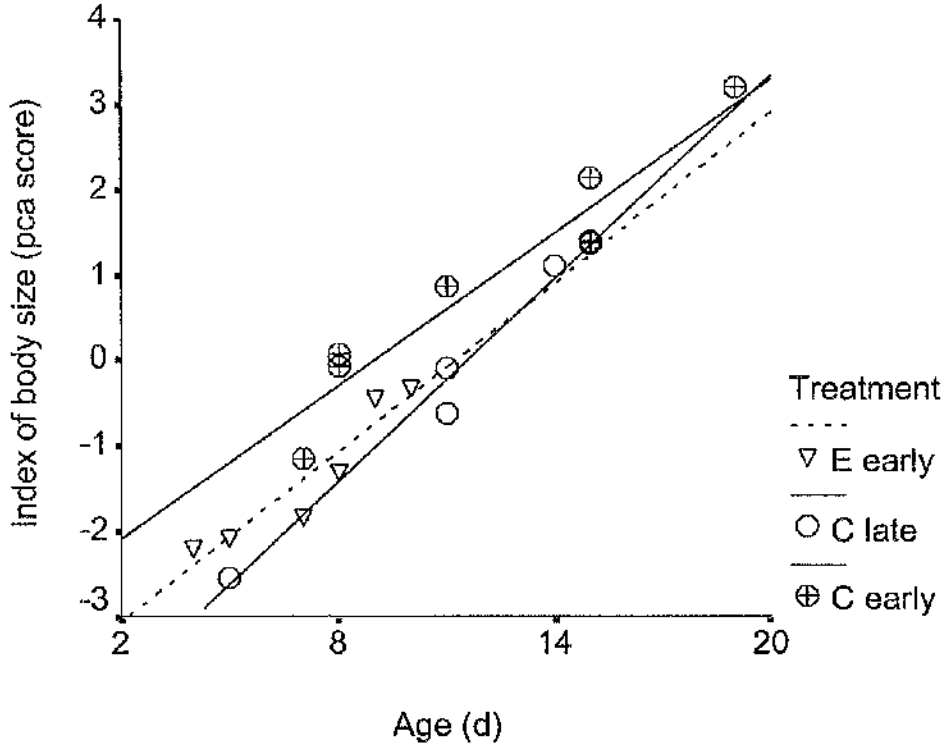
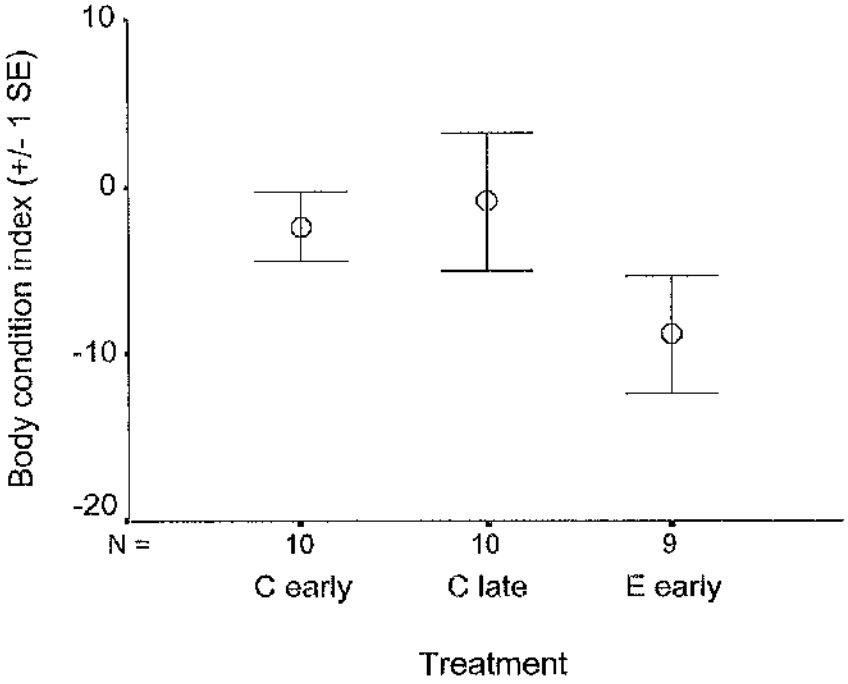

index of body size (pca score)
4
3
2
1
0
-1
-2
-3
2
8
14
20
Age (d)
Treatment
E early
C late
C early

Figure 7. Body condition index of chicks from control early (C early) and late (C late) treatments compared to chicks from the experimental early (E early) treatment, using mean residual values from predicted mass (see Methods). There was no difference between treatments (ANOVA $F_{2,26} = 1.561$, $P = 0.229$).


Body condition index (+/- 1 SE)
10
0
-10
-20
N =
10
10
9
C early
C late
E early
Treatment

Discussion

The results of this study agree with the prediction that fitness consequences of egg loss are relatively severe in poor conditions. Reproductive success was reduced in replacement eggs, especially in birds whose first egg was laid after the median laying date. However, even in relatively early-laying birds, most of whom laid a replacement egg, reproductive success was poor. Other workers have experimentally demonstrated that high-quality (early-laying) guillemot pairs that lay a replacement egg can have at least equal reproductive success compared to pairs that lay only a first egg; usually over 70% success (Hatchwell 1991; Hipfner 1997). In non-experimental studies of the breeding success of pairs producing replacement eggs, which may be biased toward poor quality birds, the mean success of replacement eggs tends to be less than that of first eggs (mean success of replacement eggs ca. 30-40%; reviewed in Murphy & Schauer 1994). This implies that replacement laying is normally not a demanding process for high-quality guillemots, but that low-quality, often late-laying, guillemots losing their first eggs face a reduction in reproductive success. A partially similar trend was present in our results, with the E early treatment, which presumably contained higher-quality pairs, having higher relaying probability and replacement-egg hatching success than the late-laying E late treatment. However, due to severely diminished fledging success, the reproductive success arising from replacement eggs of even the earliest-laying birds in our study was much lower than that in previous studies (<20%, compared to ca. 70%; Hatchwell 1991; Hipfner 1997; Hipfner *et al.* 1999; but see Hedgren 1980) and lower than even the mean success of replacement eggs.

This decrease in success of replacement eggs could be most parsimoniously ascribed to two effects: normal seasonal decline in productivity, and asynchrony of

the replacement eggs arising from the experimental protocol. Seasonal declines in success are commonly reported for this species (Birkhead & Nettleship 1987; Hatchwell 1991; Wanless & Harris 1988) and are a general feature in many avian taxa (Daan *et al.* 1988; Perrins 1970). The reproductive success of both control treatments in this study did not vary over the season (Fig. 3), but the reproductive success of the colony as a whole did decline over the season, based on data from productivity plots monitored as part of a related study (Fig. 3). However, the reproductive success of replacement eggs was much lower than would be expected from the general seasonal decline, and we can therefore rule out simple environmental degradation over the duration of the season as the proximate cause of reduction in replacement egg success (Fig. 3).

The relative date of laying within subcolonies has been demonstrated in this species to generally be of greater importance than date relative to the colony as a whole (Wanless & Harris 1988; Hatchwell 1991), and it could be argued that reduced success of replacement eggs in this study is due simply to their being laid too far out of the normal synchrony. However, other experiments using a similar approach but at healthier colonies yielded different results: at the Isle of May, Scotland, 60-70% of eggs lost 10 d past median laying were replaced (Wanless & Harris 1988), compared to 36% replacement of the E late eggs we removed 10 d after median laying; while at Skomer, Wales, 50-60% of eggs lost 10 d after median laying were replaced, and furthermore even those replacement eggs that were laid 14 d after median laying yielded ca. 50% productivity (Hatchwell 1991), compared to our 16% productivity of E early replacement eggs laid 14 d after median laying. In work on Brünnich's guillemot at Coats Island, Canada, one study showed that only 10% of eggs lost 10 d after median laying were relaid; however, the productivity of those eggs that were replaced was very high, with replacement eggs from older, earlier-laying pairs that

were laid ca. 12-14 d after median laying having ca. 70% reproductive success (De Forest & Gaston 1996). A second study showed that replacement eggs from high-quality birds laid ca. 14 d after median laying had >= 50% reproductive success (Hipfner 1997). None of these studies experienced unusually prolonged laying periods, and all reported good conditions or expanding populations. Therefore we conclude that reduced synchrony does not in itself cause poor breeding performance, and our data suggest that the cost of replacement laying is higher in poor conditions.

We invoke two non-exclusive hypotheses to explain the severity and pattern of replacement laying effects in this study. The 'seasonal hypothesis' holds that declines in productivity are caused by date effects and are independent of pair quality, while the 'quality hypothesis' states that declines result from parental quality effects and are independent of date (Hipfner *et al.* 1999). The lack of a date-related trend in fitness among the control pairs indicates that neither parental quality nor seasonal changes affect the fitness of first eggs at this sub-colony in a gradual fashion. The similarity in hatching success between control pairs and between E early pairs (rearing replacement eggs ca. 9 days later than C late pairs) provides further evidence for lack of gradual season- or quality-related date effects, particularly given that declining hatching success normally drives seasonal productivity declines in this species (Wanless & Harris 1988; Boekelheide *et al.* 1990).

However, the severe reduction in the success of experimental pairs indicates that there is a date-related threshold limiting fitness, irrespective of parental quality. The chicks of E early pairs were gaining mass at least as quickly as chicks from control pairs, but disappeared from nests prior to fledging. This indicates that the parents of chicks from replacement eggs were neither restraining their investment in terms of provisioning effort, nor was their investment overtly constrained by insufficient food availability or by the added costs of producing a replacement egg.

Previous studies on guillemots have shown that chicks from replacement eggs can grow as well as chicks from first eggs, even when hatching later than first eggs (de Forest & Gaston 1996; Hatchwell 1991), suggesting negligible costs of egg production in this species, but other work has shown decreased growth (Hedgren & Linnman 1979; del Nevo 1990), suggesting mediation by environmental conditions. But despite apparently normal chick growth in this study, the observed abandonment of experimental chicks may represent the kind of constraint/restraint threshold proposed by Curio (1983), whereby constraints are used as a facultative yardstick to gauge reproductive restraint. Clutch abandonment has been shown to be a state-dependent decision in penguins (Olsson 1997) and in terns (Monaghan *et al.*1992) and should occur when the cost of attending the nest results in a reduction of parental fitness (Stearns 1992; Fernandez & Reboreda 2000). The body condition of the experimental groups did not differ at the start of the experiment, but the early-laying experimental group may have been more willing to expend resources in replacement breeding because they were more capable of regaining lost condition and therefore more willing to reduce their body condition in the short term (Drent & Daan 1980; Olsson 1997).

There was a significant decline in first egg size as the breeding season progressed. The decline was greater in dry mass terms than in egg volume terms; we use dry mass as a more accurate measure, since the relative nutrient content of eggs have been shown to change independent of egg volume (Nager *et al.* 2000). Egg size declines have previously been interpreted as either a constraint due to seasonal deterioration of food resources, a consequence of younger, poorer-quality females breeding later, or, alternatively, as an adaptive strategy to maximise chick fledging mass or synchrony within time constraints (Birkhead & Nettleship 1982; Hipfner 1997; Hipfner & Gaston 1999a,b). Although there is little evidence to correlate egg size and

offspring fitness, it has been shown that larger eggs tend to produce heavier chicks (i.e. with greater nutrient reserves) that are capable of enhanced growth (Hipfner & Gaston 1999b; Williams 1994) and more resistant to starvation (Hatch 1983). In the case of guillemots, increased wing growth could lead to improved post-fledging survival, since their fledging strategy depends on successfully making the transition from cliff to ocean (Daan & Tinbergen 1979; Gilchrist & Gaston 1997). Our data do not allow discrimination between seasonal and quality effects on egg size, but there is some evidence for both. The replacement eggs were correlated in size with first eggs from the same mother, showing that individual variation acts consistently in egg production over the season, but they were ca. 8 % smaller (Table 1). However, experimental replacement eggs from E early pairs were as large as first eggs from C late pairs laid ca. 10 d earlier and did not appear to follow the general pattern of seasonal decline (all replacement eggs above the first egg size-season regression; Fig. 5). This indicates that the higher quality of early-laying birds allowed them to at least partially overcome the constraints acting on later-laying birds, as has been found in Brünnich's guillemots (De Forest & Gaston 1996; Hipfner *et al.* 1997), although it is not possible to confirm this without concurrently-laid first and replacement eggs (Fig. 5). We found no relative changes in egg composition over the season or between first and replacement eggs, indicating no obvious lack of capital or income resources for egg production (Drent & Daan 1980). But it has recently been proposed that protein more directly limits egg production than does lipid, and since we did not analyse egg composition at the biochemical level there may have been differences in albumen protein composition (Meijer & Drent 1999).

The reasons behind the difference in relaying probability between the early- and late-laying treatments cannot be resolved using our data, but are likely to represent quality rather than seasonal effects. Recent work on Brünnich's guillemots has

concluded that the seasonal decline in replacement layings is due to lower-quality pairs laying late in the season, rather than a general deterioration in the environment or other date-related effects (Hipfner *et al.* 1999), and there is no evidence to argue that the situation will be different in common guillemots. However, synchrony effects are relatively stronger in common guillemots (Murphy & Schauer 1994; de Forest & Gaston 1996). Since the first eggs of late-laying experimental pairs were removed in our experiment only near the end of the normal laying period, it may be that the replacements would be laid so far out of synchrony with neighbouring pairs that the E late treatment tended to decide against replacement laying based on lack of synchrony rather than on their own condition or other environmental conditions.

The time taken to produce a replacement egg was negatively related to laying date within the E early treatment, but there was no correlation between laying date or relaying interval and change in egg size between first and replacement egg. It appears that individual variation dominates these relationships; over five years of study, Murphy and Schauer (1994) reported no correlations between relaying interval and laying date, egg loss date, or incubation duration. We would expect that earlier-laying birds (likely of higher quality) might be able to produce a replacement egg more quickly, but in fact the opposite is the case. Other workers have suggested that incubation is a relatively low-cost activity in guillemots (Gaston & Perin 1993); however, there may be hormonal changes triggered by onset of incubation that increase the time necessary to develop a replacement egg (Jacobs & Wingfield 2000); in this species, the mediation of hormonal changes in relation to quality and season is not well understood.

Taken together, results from this study provide evidence of severe within-season fitness costs of egg loss at a declining guillemot colony. The decision whether or not to relay following egg loss, and the eventual productivity of replacement eggs,

are clearly state-dependent. In terms of relaying probability, our results generally support the suggestion that individual quality effects are dominant (Hipfner 1997; Hipfner *et al.* 1999). However, this study demonstrates the importance of environmental conditions. That the effects of egg loss exceeded the effects of late breeding shows that replacement laying under poor conditions carries a fitness cost beyond gradual declines in food availability or in individual state. Reproductive success in guillemots is not normally linked to moderate changes in environmental conditions; instead, activity budgets are buffered to result in relatively constant productivity of a wide range of conditions (Piatt & Anderson 1996; Uttley *et al.* 1994). However, a threshold is sometimes reached beyond which breeding failures occur- this experiment provides support for a similar threshold operating on replacement laying. Whether the fitness cost is borne entirely by a reduction in current fecundity is unknown; we made no measurement of future reproductive costs (e.g. parental survival) and it is possible that parental compensation for egg loss at this food-stressed colony may be further expressed in reduced survival and/or reduction of future fecundity.

Chapter Six

General Discussion

General Discussion

The chapters presented in this thesis were written in the format of free-standing papers. The detailed results of each have therefore already been discussed in the relevant discussion sections. Here I briefly interpret my main findings in the context of reproductive costs and trade-offs, as presented in the general introduction.

A variety of reproductive costs were suggested in my work. Although it is important to recognise that there may be secondary benefits to 'failed' breeding (e.g. nest-site retention, mate attraction, and acquisition of breeding experience), some cost was evident in the reduced reproductive success of parents that bred late in the season. The level of parental effort was unknown in this study, but for birds laying eggs that failed to give rise to a successfully fledging chick, I infer substantial investments in nest-site defence, egg production, and chick provisioning.

My work focused on birds breeding under apparently variable conditions, given the dramatic differences in reproductive success observed across years and colonies. Independent data on variation in food availability was available on an annual scale, allowing some speculation as to the forces driving productivity differences. Assuming a broadly positive correlation between prey availability and reproductive success, my efforts to draw a link between body condition and reproductive success highlighted a key life history question: What is the extent to which productivity reflects variation in the environment versus variation in the way resources are allocated between reproduction and self-maintenance (Drent & Daan 1980; Cooch & Ricklefs 1994)? Realising solutions to this question will require more controlled work than presented in this thesis, but it is instructive nevertheless to attempt to fit our observations into the most likely scenario of balancing reproductive costs and benefits. As pointed out by Stearns (1992), understanding the demographic

consequences of variation in life histories requires no actual measurement of reproductive effort; it is more important that the quantity of reproduction (productivity) and the cost of reproduction (e.g. changes in productivity or survival) are known. However, given the difficulties of measuring reproductive costs in natural systems, an important step is to gain a fuller understanding of how one common proximate cue of reproductive costs, body condition, varies in relation to productivity. Our study (Chapter Four) has served to identify the complexities involved in that linkage.

From models of generalised life cycles, Cooch & Ricklefs (1994) concluded that even high levels of environmental variation should cause small, often undetectable changes in optimal reproductive effort. They further proposed that any changes in effort will be trivial in comparison to changes in productivity and survival. By experimentally inducing guillemots to lay a replacement egg, a significant change in reproductive effort was imposed. However, replacing lost eggs is a normal process for guillemots, and so may not reflect a significant increase of effort when considered in the long term. My experimental design sought only to test whether the increased effort within a season led to particularly harsh costs expressed in reduced productivity within the same year. My results demonstrated some state-dependence (McNamara & Houston 1996), as birds at this apparently food-poor colony were for the most part unable to successfully rear a chick when burdened with increased costs of egg production. The exact mechanism by which this operated was less clear, though I suggest that deteriorating food supplies were unlikely to be solely responsible. A large amount of work has been directed toward identifying the ultimate causes of seasonal declines in success of normal and replacement clutches, with most arguments boiling down to seasonal (i.e. purely date-related, environmental changes) versus quality (i.e. related to some inherent quality of the

individual, such as condition, provisioning ability, nest-site quality, predation avoidance, etc.) effects. Using experimental manipulations, some authors have provided strong evidence for the dominance of quality effects (Hipfner *et al.* 1998), while others have argued for seasonal effects (Siikamäki 1998). Their relative importance is likely to finally depend on an interplay between the study organism and the local conditions, and is not amenable to broad conclusions.

Despite the failure of some late-laying and most replacement-laying pairs to successfully fledge a chick, others were able to rear offspring whose condition at departure did not differ from chicks fledging earlier in the season. Were some parents trading off their own condition by working harder to provision offspring under deteriorating prey availability, while others shunted increasing costs to their offspring? Trade-offs are confounded by a number of factors, making their clear measurement very difficult to achieve (Stearns 1992). Here we have attempted to identify costs of reproduction, and have avoided the temptation to extend our results into suggestions of trade-offs.

What could we have done differently in this study to allow more complete measurement of costs and trade-offs? Firstly, more experimental variables could have been measured. The original intent was to also quantify parental effort and parental condition and examine changes resulting from manipulation. Secondly, the manipulation could have been more complex, to result in control of multiple variables. Siikamäki (1998) observed that it is not possible to manipulate only the timing of breeding; however, other authors have used egg removals and cross-fostering techniques to successfully control both timing and individual quality variables (Brinkhof *et al.* 1997; Hipfner *et al.* 1998; Daunt *et al.* 1999) while minimising the remaining confounding variables (e.g. altered incubation duration). Finally, a more comprehensive assessment of the proximate factors involved in reproduction

could have been made. Here I have presented no data on i) parental time budgets or energy expenditure, ii) offspring survival or recruitment, and iii) adult survival. Knowing something about any or all of those factors would have allowed firmer conclusions.

These missing pieces can be at least partly ascribed to difficulties of working in the chosen study system. Birds are indeed fundamentally suitable for studies of reproductive costs, trade-offs, and parental investment, but there are some problems. Birds like the guillemots studied here are very long-lived, meaning that patterns of allocation are profiled across a lifetime of reproductive effort. This greatly complicates interpretation of costs measured over one or two breeding seasons, as in this study. Birds also show variability in breeding 'strategies' (i.e. 'complex adaptations'; Stearns 1992), suggesting some phenotypic plasticity that can cloud understanding of the relationship between traits and the environment (the genotypic 'reaction norm'; Stearns 1992).

Furthermore, the fact that birds are visible and easily observed does not always offset the sheer practical difficulties of working with them in the field. There are few directly controllable variables, and manipulations run the risk of unleashing a cascade of unintended changes. Some variables simply cannot be measured, as in my inability to capture adult guillemots during the chick-rearing phase in this study. Why then has this thesis been written using guillemots as a model study system? The answer is in large part because conservation implications urged work on the species and location. Some seabird populations in the Gulf of Alaska, where the work took place, have been heavily impacted by oil pollution and other anthropogenic perturbances (e.g. gill netting) in recent years, and attempts to understand their recovery have prompted expanded work on the factors that shape population changes, and how to most effectively monitor population and marine habitat changes

(Monaghan 1996; Piatt & Anderson 1996). I have demonstrated that the costs of egg loss are severe in poor conditions; yet these are the conditions under which egg loss is likely to be highest, given that nesting density and synchrony may be reduced, and egg-predating gulls may also be suffering from food shortages and therefore may increase their predation efforts. Thus there could be greater-than-expected consequences from egg loss, especially at marginal or declining colonies that in some areas are currently of great conservation interest. My results will contribute to understanding those effects.

A further reason why guillemots are favourable for ecological study is the extensive body of work already done on the species (e.g. Nettleship & Birkhead 1985; Boekelheide *et al.* 1990; Gaston & Jones 1998), allowing greater understanding of the context in which reproductive variation takes place. As emphasised by McNamara & Houston (1996), very large complexities arise in understanding reproductive costs and optimised patterns of resource allocation in a population structured by some state variable and in a fluctuating environment, as in this study system. Further complexity results from intergenerational effects- likely to be important in a species such as the guillemot that show high philopatry. Seen in this context, my attempts to understand some of the costs of reproduction and their expression in common guillemots represent a small step, building on previous work, towards a more nuanced understanding.

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